# Applied carnivore management in a data deficient world: leopard *Panthera pardus* as a case study

By

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# ABSTRACT

Large carnivores are vital to biodiversity at a global scale, through their role as keystone species, but also present significant challenges for conservation and management due to the lack of basic information on carnivore abundance and distribution, particularly at regional and sub-continental scales. Consequently, large-scale carnivore management decisions are seldom supported by science-based evidence. In this thesis, I use leopards *Panthera pardus* as a model large carnivore, in Limpopo Province, South Africa, to investigate and address some of the fundamental components that underpin wildlife management and conservation in a landscape dominated by people. Furthermore, I develop practical and scientifically justified methods to facilitate accurate and efficient management of the species at a scale that is meaningful to leopard conservation.

I begin by developing a model approach to leopard management, particularly in the context of trophy hunting, using data that are currently available to management authorities, and provide management recommendations to improve leopard population persistence. Next, I focus on the game ranching industry—the primary driver responsible for lethal leopard control—and assess the relationship between game ranchers and free-ranging wildlife. I then explore the evolution of game ranching practices to better understand the concomitant change in game rancher tolerance of free-ranging wildlife, and integrate this mechanistic understanding into the challenges facing conservation policy making more generally. Given the challenges faced by leopards across Limpopo (e.g., high levels of trophy hunting, state-sanctioned population control, and illegal killing), I then set out to investigate leopard resource use and landscape connectivity across Limpopo to better understand leopard space use in the region. I present an efficient method of integrating connectivity within wildlife management, and in doing so, identify key conservation priorities. Lastly, given that so little is known about how species respond to hunting, I present a simulation study focused on assessing biological sustainability of leopard hunting. I demonstrate that the sustainable hunting of leopards remains a challenging objective given the high degree of additive anthropogenic mortality (i.e., illegal killing and state-sanctioned problem animal control) and challenges associated with accurately aging leopards in the field. The findings presented in this thesis provide valuable information and novel guidance that could benefit the management and conservation of leopards across the region, and further afield.

# PREFACE

The work carried out in this PhD thesis was carried out across Limpopo Province, South Africa through the School of Life Sciences, University of KwaZulu-Natal, Westville Campus, from April 2013 to June 2016, under the primary supervision of Professor Rob Slotow and Dr. Guy Balme and co-supervision of Dr. Luke Hunter.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

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# DECLARATION 1 – PLAGIARISM

I, Ross Tyzack Pitman, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.

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3. This thesis does not contain other persons’ data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

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# DECLARATION 2 – PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis (include publications in preparation, submitted, in press, and published and give details of the contributions of each author to the experimental work and writing of each publication).

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*Author contributions*: RTP conducted all fieldwork, processed and analysed the data, and designed and wrote the paper. LHS, LTBH, RS and GAB provided valuable comments on the manuscript.

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Ross Tyzack Pitman

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# CHAPTER 1 – General Introduction

The biodiversity of life on Earth (including the variation of genes, species and functional traits (Cardinale *et al.* 2012)) represent a fundamental component of ecosystem structure (Chapin *et al.* 2000). Many organisms act as ecosystem engineers by altering the physical formation of habitats (Jones 1994), biogeochemical cycles (Moe *et al.* 2005), and ecosystem productivity (Power *et al.* 1996). The loss of biodiversity could therefore substantially change the structure and functioning of whole ecosystems and compromise their ability to provide society with vital goods and services (Cardinale *et al.* 2012).

Although biodiversity is essential to life, it is under increasing threat (Brooks *et al.* 2006), with many species facing extensive range contractions and extinctions (Laliberte & Ripple 2004; Cardillo *et al.* 2005; Bates *et al.* 2014). Large terrestrial mammals play a fundamental role as ecosystem engineers through their effect on prey populations or by altering vegetation structure and species composition (Morrison *et al.* 2007). Life-history traits (Brashares 2003), large body size (Cardillo & Bromham 2001), and specialized habitat requirements (Fischer & Lindenmayer 2007) increase the susceptibility of terrestrial mammal species to local extirpation and extinction as a result of anthropogenic impact (Karanth *et al.* 2009). Moreover, conflict between people and wildlife represents one of the most critical threats to wildlife species (Dickman 2010). Over 25% of global terrestrial mammal species are now facing the prospect of extinction—either locally or globally (Carwardine *et al.* 2008). Large terrestrial mammals are now among the world's most threatened taxa (Channell & Lomolino 2000), with over 79% of the world's land surface having lost its full complement of large mammalian assemblages (Morrison *et al.* 2007).

Conservation success depends on understanding the social and ecological factors that support species persistence (Karanth *et al.* 2010), particularly in human-dominated landscapes where widespread habitat fragmentation has compromised the structure and connectivity of habitats (Zeller, McGarigal & Whiteley 2012), and thus impacted species distribution and persistence (Sanderson *et al.* 2002). In addition, conservation success requires strategies for managing whole landscapes within a systematic framework, where accurate data on biodiversity is documented, where conservation goals are identified, where efficacy of existing conservation areas is measured; where new conservation areas are established, and where scientifically justified conservation actions and management procedures are implemented (Margules & Pressey 2000).

Effective management and conservation of wildlife and their habitat is therefore an urgent requirement at a global scale (Ripple *et al.* 2014; 2015)—failure to do so may ultimately lead to a loss of system components and goods and services (e.g., provisioning of food and water, or maintaining or improving air quality; see (Balvanera *et al.* 2006) for a review) on which all life depend (Sala *et al.* 2000).

## 1.1 CARNIVORES AS CONSERVATION PRIORITIES

### 1.1.1 CHARISMATIC ECOSYSTEM ENGINEERS

Ecological theory predicts that major changes in ecosystem functioning and processes occur when carnivore populations change in abundance and distribution (Estes *et al.* 2011). Empirical work has demonstrated that ecosystems are broadly characterised by three key elements (Estes *et al.* 2011). First is the concept that carnivores shape ecosystems (Hairston, Smith & Slobodkin 1960). Commonly termed 'trophic cascades', this concept posits that carnivores impact prey populations, which, in turn, ripples downwards through food webs influencing similar or lower trophic levels (Paine 1980). A famous example of a trophic cascade was detected in Alaska between sea otters *Enhydra lutris*, invertebrate herbivores and microalgae (Estes & Duggins 1995). The study found that where sea otters occur, herbivores are rare, and plants are abundant. Their findings demonstrated that Alaskan kelp forests are dependent on sea otter predation for protection against destructive grazing by herbivores (Estes & Duggins 1995). Furthermore, in a meta-analysis conducted by Schimtz et al. (2000), trophic cascades were detected in 45 of the 60 studies they reviewed—suggesting that this phenomenon is ubiquitous throughout nature. Second, alternative stable states characterise 'tipping' points at which ecosystems are pushed—following perturbations of significant magnitude—from one state to another, resulting in abrupt changes in ecosystem structure and functioning (Lewontin 1969). Beschta & Ripple (2006) documented an alternative stable state in Yellowstone National Park, USA, following the removal of large carnivores where elk *Cervis elaphus* caused widespread loss of willow (*Salix spp.*) communities by overgrazing streamside vegetation, resulting in increased hydraulic capacity and decreased hydraulic connectivity within adjacent floodplains, that effectively changed landscape characteristics and vegetative functioning (Beschta & Ripple 2006). The final key element, interconnectedness (Schmitz, Hambäck & Beckerman 2000), suggests that every species can influence many other species through interactions across ecosystem linkages (Estes *et al.* 2011). Carnivores, in this context, play a major role. Through top-down processes, carnivores influence behavioural adaptations of their prey (Estes *et al.* 2011), regulate primary productivity by influencing herbivore populations (Terborgh *et al.* 2001), and limit the abundance of smaller carnivores (Ritchie & Johnson 2009). Humans, too, have not escaped the influence of carnivores. The meat scavenged or kleptoparasitised from carnivore kills is likely a key factor in early human development (Blumenschine 1991; Psouni, Janke & Garwicz 2012). In human cultures, carnivores have remained a subject of contention, as well as reverence, dating back to prehistoric times (Turner 1992; Clottes 2003). As charismatic species they garner significant admiration, and yet, as predators, they are intensely persecuted on a global scale (Ripple *et al.* 2014).

### 1.1.2 TROPHIC DOWNGRADING

Large mammalian carnivores are one of the most vulnerable group of mammals (Schipper *et al.* 2008; Estes *et al.* 2011), primarily due to their volatile relationship with people (Woodroffe *et al.* 2005). Large carnivores are particularly sensitive to the expansion of human populations into wild habitats (Woodroffe 2000), and, as a result, conflict between people and predators remains the greatest threat to carnivores globally (Woodroffe & Ginsberg 1998). The removal of carnivores from Nature—a process referred to as ‘trophic downgrading’ (Estes *et al.* 2011)—remains one of humankinds most pervasive influences on the natural world (Ripple *et al.* 2015). Quantifying the decline in carnivore populations represents a challenging task. On a global scale, extirpations and extinctions of carnivore populations have occurred for generations (Ripple *et al.* 2014), whilst the dynamic conditions of the natural world make it difficult to detect changes in ecosystem processes and species interactions (Estes *et al.* 2011). Therefore, the loss of carnivores often remains an invisible process (Ripple *et al.* 2014), which exacerbates further declines through the phenomenon of “shifting baselines”—where the disappearance of species is gradual and largely undetectable by biologists studying these systems over time (Pauly 1995). When their disappearance of carnivores is detectable, it is often too late to restore their populations, as well as the vital role they play as top-down regulators (Estes *et al.* 2011). A well-documented effect of shifting baselines can be seen in the increasing abundance and distribution of mesopredators across the world's ecosystems as larger carnviores are removed (Prugh *et al.* 2009). As successive stages of environmental and food-web degradation occur, we gradually become accustomed to the transformation of an intact ecosystem into an alien landscape (Baum & Myers 2004; Prugh *et al.* 2009).

### 1.1.3 THE IMPORTANCE OF SCIENCE-BASED CARNIVORE CONSERVATION

Accurately documenting the change in carnivore distribution has become a priority for conservation efforts globally (Ray, Hunter & Zigouris 2005). There is, however, a lack of basic information on carnivore abundance and distribution (Long *et al.* 2008), particularly at regional and sub-continental scales (Karanth *et al.* 2009). This dearth of information is primarily due to the difficulty in obtaining data on wide-ranging, and often elusive species (Thorn *et al.* 2011). As a consequence, large-scale carnivore management decisions are seldom supported by science-based evidence (Sutherland *et al.* 2004). Given the rapid decline of global biodiversity (Sala *et al.* 2000), conservation planning requires a systematic and adaptive approach (Margules & Pressey 2000; Westgate, Likens & Lindenmayer 2013), where current and future management decisions are furnished with evidence gathered from previous management practices (Westgate, Likens & Lindenmayer 2013). Such an approach aims to improve management of critical habitats by learning from management outcomes (Williams, Szaro & Shapiro 2009; Biggs *et al.* 2011), but can only be implemented where management actions are appropriately scaled to the ecological system of interest (Delsink *et al.* 2013; Guerrero *et al.* 2013). Carnivore conservation requires creative solutions, on a global scale, to combat the degradation of habitats and human-mediated persecution (Di Minin *et al.* 2016). There is urgent need for increased recognition of, and focus on, conserving the ecosystem effects provided by carnivores (Ripple *et al.* 2014), but these positive effects can only be sustainably harnessed if humans are willing to adapt to the presence of carnivores (Miquelle *et al.* 2005; Dickman 2010). At the same time, the impacts of carnivore persistence on humans must be minimised (Dickman 2010). Both of these aspects represent major socio-political challenges that require adaptive management decisions formulated through robust science-based evidence (Karanth *et al.* 2003; Estes *et al.* 2011; Ripple *et al.* 2014).

## 1.2 CHALLENGES FACING CARNIVORE CONSERVATION

### 1.2.1 FACTORS AFFECTING CARNIVORE PERSISTENCE

Conflict between humans and wildlife represents a pervasive conservation challenge due to competition for shared resources (e.g., meat and space) (Woodroffe & Thirgood 2005). Carnivore depredation imposes significant costs on the livelihoods of local people, whilst the expansion of human populations into wildlife habitat acts to further exacerbate levels of conflict (Woodroffe & Thirgood 2005; Goswami *et al.* 2015). Although the retaliatory killing of carnivores—in response to confirmed or assumed depredation events—remains a concerning source of conflict (Dickman 2010), pre-emptive killing of carnivores represents an even greater source of conflict that appears deep-rooted within the human psyche (Kansky, Kidd & Knight 2014). Accordingly, the attitudes, perceptions, and tolerance of people towards carnivores plays a vital role in wildlife conservation efforts and presents one of the primary areas of interest for conservation practitioners (Kansky, Kidd & Knight 2014; Selinske *et al.* 2015).

Human-wildlife conflict is closely linked to economic factors (Dickman 2008; 2010), and, for carnivores more specifically, to the financial loss of revenue through property damage and stock depredation (Nyhus *et al.* 2005; Thorn *et al.* 2013). The cost of coexisting with wildlife is rarely offset by the benefits (Balmford & Whitten 2003), and, as a result, tolerance of wildlife among landowners and communities is often low (Walpole & Thouless 2005). Human impact on biodiversity is largely determined by socioeconomic factors such as land tenure systems, poverty, market pressures and regulatory frameworks (Chomitz 2007; Holland, Peterson & Gonzalez 2009), which have direct or indirect implications for species persistence (Bond *et al.* 2004). For instance, across southern Africa, legislation imposed during the colonialist period established centralized control over wildlife populations (Bond *et al.* 2004; Child 2012a). This control, which was based on the political economic philosophy set out by the 1933 London Convention (Child 2012b), limited the commercial use of wildlife (Lindsey, Romanach & Davies-Mostert 2009a)—effectively diminishing the value of wildlife, and, by contrast, making them a financial burden (Murombedzi 2003; Child 2012b). As a result, wildlife populations declined due to persecution, poaching, and competition for resources (Lindsey, Romanach & Davies-Mostert 2009a; Child 2012b). During the 1960s and 1970s, new legislative policies bestowed custodial rights of wildlife to the landowner (Lindsey, Romanach & Davies-Mostert 2009b; Child 2012b). These legislative changes allowed landowners to derive financial benefits from wildlife occurring on their properties (Bond *et al.* 2004). This encouraged innovation among the private sector who began to champion a 'use it or lose it' philosophy (Child 2012b), resulting in a major land-use change from livestock farming to commercial game ranching (Bothma, Suich & Spenceley 2009; Child 2012c; d). Although game ranching is perceived to benefit wildlife conservation (Cousins, Sadler & Evans 2010), considerable concern exists over the viability of carnivore populations occupying land-use types designated for the commercial production of wild game due to the high risk of intolerance among game ranchers towards carnivore species that may threaten their game (Lindsey, Dutoit & Mills 2005).

One of the primary causes of habitat degradation and the loss of habitat connectivity is land-use change (e.g., shift from livestock farming to game ranching; as mentioned above), which presents a significant form of global pressure affecting biodiversity (Sala *et al.* 2000; Zebisch, Wechsung & Kenneweg 2004). Transformation of land, and how land is managed, are key drivers of biodiversity loss at global, national and local scales (Haines-Young 2009), and forms a central component of global environmental and sustainability research (Turner, Lambin & Reenberg 2007). Landscape degradation, fragmentation and the loss of habitat connectivity has led to the global population decline of numerous mammalian species (Ceballos & Ehrlich 2002), of which large carnivores are the most severely impacted (Crooks *et al.* 2011). Accurately quantifying habitat connectivity remains a fundamental component of successful conservation (Zeller, McGarigal & Whiteley 2012). However, although important, connectivity is poorly integrated within conservation planning and wildlife management, not least because connectivity is so challenging to measure and requires datasets that are often not readily available to conservation authorities (Martin *et al.* 2012; Zeller, McGarigal & Whiteley 2012). Given the challenges in measuring and maintaining habitat connectivity, many carnivore species have undergone widespread extirpation or localized extinction across their historic geographical range as a direct result of anthropogenic pressure (Cardillo *et al.* 2004; 2005). Across Africa, carnivores have experienced an average range loss of 36%, where only 14% of the total land area is comprised of intact medium and large felid communities (Ray, Hunter & Zigouris 2005).

The conservation and management of natural resources requires careful consideration of not only wildlife and the habitat in which they occupy, but also the human perspective (Slotow & Hunter 2008). However, societal responsibilities may not always fully align with conservation objectives (Delsink *et al.* 2013). For example, the scale at which natural resources are managed can sometimes be vastly different to the scale at which society implements management strategies (Vatn & Vedeld 2012; Delsink *et al.* 2013). When the scale of management actions and the scale of biological processes do not match (termed 'scale mismatching' (Cumming, Cumming & Redman 2006)), inefficiencies and failed conservation objectives often result (Cumming, Cumming & Redman 2006; Guerrero *et al.* 2013). For carnivores that range over large distances, scale mismatching represents a significant threat to their management and conservation. It remains that large-scale carnivore management decisions (e.g., prioritization of critical habitats, or allocation of limited resources) are seldom supported by science-based evidence (Sutherland *et al.* 2004; Artelle *et al.* 2014). As a prime example, although management zones feature prominently in conservation planning, they are often demarcated along administrative boundaries, rather than ecologically meaningful geographical features (Stoner *et al.* 2013). Such inadequacies in management scale can have severe conservation implications (Guerrero *et al.* 2013), and ultimately lead to declining carnivore populations (Chundawat *et al.* 2016).

Consumptive utilisation (e.g., sport hunting) remains an important factor responsible for decreasing carnivore numbers (Whitman *et al.* 2004; 2007; Balme *et al.* 2010; Packer *et al.* 2011). Although sport hunting provides opportunities to generate revenue though wildlife utilisation (Lindsey *et al.* 2012), the lack of information on the ecological impact of sport hunting practices, together with the lack of longitudinal data of sport hunted species, typically leads to unsustainable practices (Lindsey *et al.* 2007). Quota setting decisions, for instance, are often based on very little or no scientific data (Edwards *et al.* 2014), leading to unsustainable quotas (Selier *et al.* 2014). Because of these data deficiencies, relative abundance indices (e.g., catch-per-unit-effort) (Edwards *et al.* 2014), and strict harvest strategies (e.g., age minimum or sex-specific hunting restrictions) (Whitman *et al.* 2007; Packer *et al.* 2011; Balme, Hunter & Braczkowski 2012; Palmer, Fukuyama & Relman 2015), are often adopted to inform sport hunting guidelines. Yet, the ecological and economic sustainability of these harvest strategies remains contentious (Di Minin, Leader-Williams & Bradshaw 2015; Ripple, Newsome & Kerley 2016; Di Minin, Leader-Williams & Bradshaw

2016). Sport hunting can theoretically foster tolerance of carnivores (Lindsey *et al.* 2006; 2007), and represents the most profitable form of consumptive wildlife utilisation (Lindsey *et al.* 2006). Local people and communities that live with carnivores must, however, benefit from sport hunting practices to make this a viable 'conservation tool' (Lindsey *et al.* 2006; Jorge *et al.* 2013). In addition, poorly regulated sport hunting can drive maladaptive habitat selection (Delibes-Mateos, Ferreras & Gaona 2001), where hunted species experience higher mortality in habitats that should typically confer increased fitness, and thus survival (van der Meer 2011; van der Meer *et al.* 2014). Empirical studies have shown that hunter selection can also drive changes in species morphology, resulting in rapid artificial evolution (Pigeon *et al.* 2016). Recovery through natural selection is either slow or non-existent, and, therefore, any changes to the evolutionary make-up of hunted populations can lead to permanently fixed deleterious effects (Pigeon *et al.* 2016).

Killing carnivores for cultural regalia (e.g., leopard skins for cultural ceremonies) represents a unregulated form of consumptive utilisation that may potentially affect carnivore populations (Hunter, Henschel & Ray 2013), yet this form of illegal killing remains very difficult to quantify, and thus very poorly researched. Finally, depletion of natural prey by people represents another factor attributing to carnivore declines (Henschel *et al.* 2011). Bush-meat hunters primarily target large-bodied species, resulting in marked declines in medium and large ungulates and primates (Henschel *et al.* 2011; McNamara *et al.* 2015). These trends tend to occur at higher frequencies closer to human settlements, where hunting effort is higher (Lindsey *et al.* 2013a). As the prey base depletes, carnivores are forced to switch to smaller prey or move out of an area in search of areas less inhabited by people, and thus higher in density of ungulate and primates of suitable size (Henschel *et al.* 2011).

### 1.2.2 DETECTING CHANGE

Large carnivores are vital to biodiversity at a global scale through their role as keystone species (Miller *et al.* 2001; Estes *et al.* 2011), but also present great challenges for conservation and management (Ray, Hunter & Zigouris 2005). Enumeration of large carnivores is a particularly difficult task due to their naturally low densities (Obbard, Howe & Kyle 2010), wide-ranging distribution and elusive nature (Hunter & Barrett 2011). Nevertheless, large carnivore monitoring is essential to their conservation, particularly due to the widespread degradation of suitable habitat for predators (Ray, Hunter & Zigouris 2005). As a result, detecting population change forms a central component of wildlife management (Caughley & Sinclair 1994), and, thus, conservation practitioners require reliable and efficient methods of monitoring population trends at large spatial scales to ensure informed decision-making (Barea-Azcón *et al.* 2006).

Typical population estimator methods (i.e., involving direct observations) include aerial surveys (Kingsford & Porter 2009), live trapping (Flowerdew *et al.* 2004), and camera-trapping (Rich *et al.* 2014). However, given the effort and resources required (Balme, Hunter & Slotow 2009), these methods are often only feasible at small scales (Barea-Azcón *et al.* 2006). In contrast, measuring indices of population change, such as sign surveys (Ausband *et al.* 2014), harvest effort (Gese 2001), trophy quality (Croes *et al.* 2011), and occupancy (Karanth *et al.* 2009), provide a way of monitoring at scales large enough to inform management (Yoccoz, Nichols & Boulinier 2001). Although population estimators and population indices are suitable for the management and conservation of wildlife, little is known of how one relates to the other (Choate, Wolfe & Stoner 2006). When comparing the efficiency at detecting mammal species richness and abundance, Silveira et al. (2003) found that track counts performed better than camera-trapping and direct faunal counts. In the Mediterranean basin, scent stations and sign surveys were more efficient methods, both economically and logistically, at detecting carnivore species, than the use of camera-trapping and live trapping when conducted at large spatial scales (Barea-Azcón *et al.* 2006). When sampling bat species in Catalonia, Flaquer et al. (2007) suggest the use three survey methods (bat detectors, mist nets and roost surveys) when assessing species richness to prevent underrepresenting bat communities.

Identifying methodologies that increase the precision, accuracy and rigour of monitoring techniques lies at the forefront of conservation management (Brashares & Sam 2005). Monitoring methods that are the most accurate, and thus the most desirable, are often the least economical (Danell & Andrèn 2010). Therefore, a compromising trade-off between monitoring cost and reliability is often warranted (Field, Tyre & Possingham 2005). The interchangeable relationship among monitoring precision, monitoring power and the frequency of monitoring intervals are three crucial components to consider when devising optimal monitoring strategies (Gerrodette 1987; Brashares & Sam 2005; Hauser, Pople & Possingham 2006; Danell & Andrèn 2010). A monitoring program that infers the lowest cost, but still facilitates reliable management decisions, is essential for a sustainable monitoring framework within an optimal management strategy (Danell & Andrèn 2010; Milner-Gulland 2011; Westgate, Likens & Lindenmayer 2013; Bunnefeld *et al.* 2013). Evaluating the statistical power and precision of monitoring estimates is important during the design and implementation of a monitoring framework, as it avoids wasted time and effort on activities that are unlikely to yield useful results (Gerrodette 1987). The precision, or reliability, of monitoring estimates is directly related to how frequently monitoring surveys are required (Danell & Andrèn 2010). Furthermore, monitoring intervals have been shown to be less important to monitoring performance than monitoring precision (Danell & Andrèn 2010). Similarly, an adaptive monitoring approach that considers the current state of the ecological system has been shown to outperform fixed-interval monitoring (e.g., annual surveys) when deciding on how frequently to conduct economically costly surveys (Hauser, Pople & Possingham 2006).

Capture-recapture techniques using camera-traps have become a highly effective and rigorous method used to count large carnivores (Karanth *et al.* 2004; Balme, Hunter & Slotow 2009; O'Connell, Nichols & Karanth 2011), but, although camera-trapping must be conducted at scales large enough to ensure unbiased population estimates (Tobler *et al.* 2008), these scales are often too small to inform wider population management (Beausoleil *et al.* 2013). In contrast, occupancy modeling techniques have shown to be very useful at monitoring large carnivore populations at provincial (Thorn *et al.* 2011; Rich *et al.* 2013; Ausband *et al.* 2014) and national scales (Karanth *et al.* 2009; 2010)—primarily because occupancy modeling relies on data that are often cheaper and easier to obtain than demographic data (Thorn *et al.* 2010). Similarly, for carnivores that undergo harvest, catch-per-unit-effort and trophy quality can be used to monitor population trends (Gese 2001; Edwards *et al.* 2014), but their relationship to true population size remains uncertain (Robinson & DeSimone 2011; Chomba *et al.* 2014). For instance, Chomba et al. (2014) demonstrated that the skull size (a potential indicator of trophy quality; i.e., over-harvested populations should theoretically exhibit smaller skull sizes as older individuals are preferentially selected over younger, less desired trophies) of lions *Panthera leo* harvested in Tanzania, Zambia, and Zimbabwe did not decline as population numbers were alleged to reduce over the same period.

### 1.2.3 SCIENCE-BASED ADAPTIVE MANAGEMENT

The human-mediated global decline of biodiversity—often termed the 'sixth mass extinction' (Wake & Vredenburg 2008)—requires efficient and scientifically-informed management of wildlife populations (Westgate, Likens & Lindenmayer 2013). The general consensus holds that management should be both a pre-emptive and reactive process that considers current and past management decisions when deciding on future management actions (Westgate, Likens & Lindenmayer 2013). The concept that epitomises this process is known as 'adaptive management', which adopts a 'learning by doing' approach and aims to integrate applied management with learning (van Wilgen & Biggs 2011). Successful adaptive management, however, requires a number of key components. First, well-designed monitoring programs are a prerequisite (Tobler & Powell 2013a). Accurate monitoring ensures that adequate data for the target population are collected so that population trends can be deduced (Ahumada, Hurtado & Lizcano 2013). Second, management practices should be implemented that are grounded in science-based evidence (Artelle *et al.* 2014), as a direct result of the data collected on population trends (Balme *et al.* 2010). Third, after a specified time-scale—typically every year—the performance outcomes of current management practices should be assessed and evaluated (Bunnefeld & Keane 2014a; Bunnefeld, Redpath & Irvine 2015). Lastly, knowledge gained from evaluating the current management system should be used to adjust management actions to enhance effectiveness (Westgate, Likens & Lindenmayer 2013; Bunnefeld, Redpath & Irvine 2015). Although often omitted, successful adaptive management typically involves the inclusion of multiple stakeholders who hold different motivating values (e.g., sport hunting versus photographic tourism) (Milner-Gulland 2011; Westgate, Likens & Lindenmayer 2013). In doing so, stakeholder inclusion ensures compliance of the management protocol (Bunnefeld *et al.* 2013). Aside from the difficulties in monitoring carnivore populations (mentioned above), stakeholder compliance (e.g., adherence to regulations) remains one of the greatest challenges facing carnivore conservation (Milner-Gulland *et al.* 2010). The management of carnivores is typically carried out in two ways: (1) by regulating sport hunting (Whitman *et al.* 2004; Robinson *et al.* 2008; Balme *et al.* 2010), and (2) by controlling problem animals (defined here as animals that cause, or are perceived to cause, damage to property or threaten human life) (Dickman 2010). In this context, managing problem animals does not simply refer to the lethal control of a species, but includes other mitigating measures necessary to reduce conflict; e.g., implementation of compensation schemes (Bulte & Rondeau 2005), adjusting husbandry practices (Shivik 2006), translocation (Athreya *et al.* 2011), or controlling access to resources (Shivik 2006). Nevertheless, both of these approaches require some degree of compliance by the general public. For instance, sport hunting requires that only certain individuals from a population are harvested (e.g., only males, only above a certain age) (Whitman *et al.* 2004); and, for problem animals, afflicted landowners are required to use effective husbandry practices, and report any conflict events so they can be handled by an official (Thorn *et al.* 2013), rather than be illegally dealt with by the landowner (St John *et al.* 2012). To ensure compliance, management authorities must engender a sense of trust between the local community and the authority that governs them (Bunnefeld *et al.* 2013). To achieve this, stakeholder-inclusive adaptive management can play a pivotal role (Bunnefeld & Keane 2014a). One of the best examples of such an approach is now widely used within fisheries. Commonly termed 'monitoring strategy evaluation' (MSE), this approach incorporates both social and ecological dynamics, and seeks to model a suite of management scenarios (Butterworth & Punt 1999; Bunnefeld, Hoshino & Milner-Gulland 2011). The modelled system can be predicted forward in time, and then assessed as to its performance and propensity to reach desired targets for each stakeholder group (Bunnefeld, Hoshino & Milner-Gulland 2011). MSE incorporates dynamics from all aspects of the system, including compliance by stakeholders (Bunnefeld & Keane 2014a). A further strength of MSE is in its ability to accommodate uncertainty at every stage of the modelling process (Bunnefeld, Redpath & Irvine 2015). Although widely used in fisheries, MSE is only recently being adopted within terrestrial systems. For example, Bunnefeld et al. (2013) used MSE to investigate trophy hunting of mountain nyala *Tragelaphus buxtoni* to assess scenarios of investment by stakeholders into anti-poaching and monitoring. Using a similar MSE approach, Edwards et al. (2014) set sustainable quotas for African lion *Panthera leo* using an index of abundance—the time it takes for a hunter to kill a lion. For carnivores in particular, two conflicting objectives exist for sport hunting: first, prevent population decline; and second, increase revenues generated by hunting (Lindsey *et al.* 2007). Without MSE, these two competing objectives would present quite a challenge for conservation practitioners (Milner-Gulland *et al.* 2010). However, the MSE approach is able to balance competing interests, particularly when uncertainty is high, to develop a range of management strategies available to stakeholders (Bunnefeld, Hoshino & Milner-Gulland 2011). MSE presents a significant advancement towards conservation science, and is likely to feature in other terrestrial systems where species are managed under uncertainty (Bunnefeld, Hoshino & Milner-Gulland 2011).

## 1.3 LEOPARDS AS A CASE STUDY

### 1.3.1 RATIONALE FOR THIS STUDY

In this thesis, I use leopards *Panthera pardus* as a model large carnivore, in Limpopo Province, South Africa, to investigate and address some of the fundamental components that underpin wildlife management and conservation in a landscape dominated by people. Leopards are the world's most wide-ranging, and persecuted felid (Hunter, Henschel & Ray 2013), and are currently listed as 'near threatened' on the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (Henschel *et al.* 2008). Twelve African countries are permitted to export a quota of leopard skins procured through trophy hunting (Balme, Slotow & Hunter 2010). While trophy hunting is regulated, there is little scientific input on the allocation of harvest quotas or the implementation of hunting practices (Balme *et al.* 2010). Accordingly, the biological sustainability of leopard hunting remains largely unknown (Packer *et al.* 2009). Leopards are also frequently killed—both legally and illegally—for their role as predators of livestock, game species, and occasionally people (Hunter, Henschel & Ray 2013). Human-wildlife conflict is a major concern for biodiversity conservation (Woodroffe *et al.* 2005) and large felids such as lion *Panthera leo* (Ogada *et al.* 2003; Holmern, Nyahongo & Røskaft 2007), leopard (Ogada *et al.* 2003; Thorn *et al.* 2013), jaguar *Panthera onca* (Zimmermann, Walpole & Leader-Williams 2005) and tiger *Panthera tigris* (Miquelle *et al.* 2005) are frequently implicated in conflict events centred around livestock and game depredation (Sillero-Zubiri & Laurenson 2001). In addition, illegal practices such as cage trapping, poisoning, shooting, and snaring constitute a significant portion of leopard mortality in Limpopo, and southern Africa more generally (Ray, Hunter & Zigouris 2005; Swanepoel 2009; St John *et al.* 2012). Poaching leopards and the illegal trafficking of their skins for cultural regalia represents another significant threat to the species (Hunter, Henschel & Ray 2013). Even though a large proportion of Limpopo is considered suitable leopard habitat (63%; which comprises 32% of suitable leopard habitat in South Africa; see Swanepoel et al.

2013), there are uncertainties regarding leopard population viability (Daly *et al.* 2005; Swanepoel *et al.* 2013). Given the tenacity of leopards in human-dominated landscapes, they present an ideal opportunity to assess the effects of human-mediated disturbance on large carnivores.

Within this thesis, I specifically address the following objectives:

1) Given that applied management of leopards is largely ad hoc and guided by limited scientific data (Balme *et al.* 2010), I develop a model approach to leopard management, that is both spatially and temporally relevant (particularly for trophy hunting and problem animal control) using the most recent scientific data to guide management of the species at provincial and national scales.
2) Given that one of the primary causes of leopard population decline is the lethal control of putative problem animals (identified in the first objective) (Pitman *et al.* 2015), I further investigate the relationship between game ranchers (a significant land use type across the region in frequent conflict with large carnivores (Lindsey, Dutoit & Mills 2005)) and free-ranging wildlife to identify the drivers that threaten their coexistence.
3) Given the fragmented nature of the study area (Swanepoel *et al.* 2013), the need for clearly defined leopard management units (identified in the first objective) (Pitman *et al.* 2015), and the need for increased regulation as a result of intensive land use practices (identified in the second objective) (Pitman *et al.* 2016), I further investigate how leopards use resources (at multiple scales) across the landscape and assess the interconnectedness of leopard management units identified in the first objective.
4) Given that our knowledge of hunting systems is so limited (Caro *et al.* 2009; Edwards *et al.* 2014), and the biological and economic sustainability of leopard hunting and lethal problem animal control is often called into question (a focus within the first objective) (Pitman *et al.* 2015), I further investigate the feasibility of sustainable recreational hunting, and other additive forms of human-mediated leopard mortality, using a simulation study.

### 1.3.2 STUDY AREA

Limpopo is the 5th largest province in South Africa (ca. 125 754 km$^2$) and is generally characterized by dry deciduous and bushveld habitats (Mucina & Rutherford 2006). Climate differs throughout Limpopo, but can be regarded as semi-arid. Temperatures average 21–22 °C in summer (peak – January), and fall to 11 °C in winter (peak – July). Precipitation averages 530 mm per annum (range: 200–1200 mm) (Institute of Soil, Climate and Water). In comparison to other provinces in South Africa, Limpopo contains extensive leopard habitat, with widespread leopard populations (Swanepoel *et al.* 2013). Limpopo awards the largest number of Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) permits (n = 52; 35% of the annual national quota) to individuals wishing to hunt leopards (Daly *et al.* 2005). Leopards can only be legally killed by a private individual who is in possession of a CITES tag or damage-causing animal (DCA) permit (also known as a destruction permit) issued by the Limpopo Department of Economic Development, Environment and Tourism (LEDET). The legal killing of leopards (both as trophies and as damage causing animals) in Limpopo is likely eclipsed by illegal offtake of leopards by farmers and poachers (Chase-Grey 2011). Most anthropogenic pressure is located along the western and north-western regions of Limpopo (Lourens Swanepoel, *unpublished data*). Instead of being evenly distributed across the province, these clustered, high mortality areas can create localized population sinks that can have devastating impact on metapopulation persistence (Robinson *et al.* 2008, Balme *et al.* 2010).

### 1.3.3 THESIS OVERVIEW

The primary objective of this thesis is to significantly increase our knowledge of leopards across a vast and biodiverse region of southern Africa, and to develop practical and scientifically justified methods to facilitate accurate and efficient management of the species at a scale that is meaningful to leopard conservation. Chapters 2–5 have been written as independent papers. These four data chapters are briefly explained below, including a sixth chapter where I synthesize my findings and explore their broader applicability:

***Chapter 2*** begins by developing a model approach to leopard management, particularly in the context of trophy hunting, using data that are currently available. I use an approach previously applied to cougar *Puma concolor* to identify *de facto* refugia and ecological traps for leopard populations at multiple scales. Using historical trophy hunting and problem leopard permit records, I assess the relationship between human-mediated leopard mortality and habitat quality, and then assess the compounding effect of multiple forms of offtake. Leopard management in Limpopo has historically resulted in clustered offtake (i.e., the legal and illegal killing of leopards in concentrated areas); I therefore suggest improvements upon the status quo by distributing trophy hunting practices in a more sustainable manner.

***Chapter 3*** focuses on the game ranching industry—the primary driver responsible for lethal leopard control—and assess the relationship between game ranchers and carnivores. I assess whether the conservation potential of game ranching, and a decentralized approach to conservation more generally, may be undermined by an increase in human-wildlife conflict. I then explore the evolution of game ranching practices from extensive to intensive, to better understand the concomitant change in game rancher tolerance of free-ranging wildlife, and integrate this mechanistic understanding into the challenges facing conservation policy making more generally.

In **Chapter 4** I estimate resource use and landscape connectivity across leopard range in Limpopo. Although globally recognised, connectivity is often poorly considered, or simply does not feature, within wildlife management. I estimate resource use across three orders of selection, and further develop a landscape-scale depiction of habitat connectivity across a vast, and highly biodiverse, region of southern Africa. I present an efficient method of integrating connectivity within wildlife management, and, in doing so, identify key conservation priorities. I demonstrate how conservation authorities can accommodate complex wildlife-habitat relationships within a single framework capable of generating accurate predictions of resource use necessary for applied management, but which are optimized for both finer- and coarser-scaled management objectives applicable to the study species and other trophic levels reliant on similar habitat types.

Little is known about how species respond to hunting (Loveridge *et al.* 2007; Caro *et al.* 2009; Edwards *et al.* 2014). Questions therefore remain over which leopard hunting strategies are the most biologically and economically sustainable. In **Chapter 5** I present a simulation study focusing on assessing a myriad hunting scenarios comprising: (a) no hunting, (b) male and female harvest, (c) male-only harvest, (d) age-restricted male harvest with and without aging uncertainty, (e) addition of recovery periods (i.e., hunting followed by non-hunting periods to allow population recovery) (Creel *et al.* 2016), and finally (f) the addition of illegal killing and/or state-sanctioned lethal control of leopards as a stochastic additive process. I demonstrate that the sustainable hunting of leopards remains a challenging objective given the high degree of additive anthropogenic mortality (i.e., illegal killing and state-sanctioned problem animal control) and challenges associated with accurately age leopards in the field. Contrary to previous research, I further demonstrate that even when hunting is restricted to male leopards ≥7 years, leopard populations continue to decline (due to the inclusion of aging error by hunters into model projections). Although I investigate the sustainability of various leopard hunting scenarios, the challenges faced by leopard management are equally present in other terrestrial hunting systems—particularly large- and medium-sized felids—for which this approach is directly applicable or contributes theoretically.

Finally, in **Chapter 6**, I will discuss the implications of these findings in the wider context of sustainable management and how this work contributes to the field of conservation and management of large carnivores more broadly.

# CHAPTER 2 – The importance of refugia, ecological traps and scale for large carnivore management

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## 2.1 ABSTRACT

Management zones feature prominently in conservation planning, particularly at large spatial scales, but prioritization of areas of concern is required to focus efforts and limited resources. Human-mediated mortality constitutes a major threat to species persistence, particularly for widespread carnivores that undergo harvest and population control, such as the leopard (*Panthera pardus)*. In this study, we evaluated the extent and spatial distribution of legal anthropogenic offtake of leopards to identify *de facto* refugia and ecological traps across Limpopo Province, South Africa. We defined refugia as management units with offtake levels below an established sustainable harvest rate, and ecological traps as management units with offtake exceeding the sustainable harvest rate. We assessed offtake at three geographical scales using trophy hunting permit records alone, and then in combination with problem leopard permit records to investigate the compounding effect of additional forms of offtake and the potential for management scale mismatching. Across Limpopo Province, high leopard offtake created fewer areas of refuge than ecological traps. Refugia were smaller in size and within close proximity of ecological traps. Human-mediated leopard mortality occurred mostly in prime leopard habitat. Finer-scaled management units resulted in fewer ecological traps and more refugia, and enables authorities to focus conservation attention in areas of concern. Human-mediated leopard mortality exceeded the annual offtake rate considered sustainable. Our study highlights the importance of assessing both the scale and distribution of the harvest, whilst also considering alternative forms of offtake, when devising harvest management strategies. Management scale mismatching and high human-mediated leopard

mortality is of particular concern in Limpopo Province, as such, we propose an adaptive, science-based regulatory framework aimed at improving leopard harvest strategies.

## 2.2 INTRODUCTION

Large-scale management decisions are seldom supported by science-based evidence (Sutherland *et al.* 2004). Given the rapid decline of global biodiversity (Sala *et al.* 2000), conservation planning requires a systematic and adaptive approach where the implementation of scientifically informed management zones feature prominently (Margules & Pressey 2000; Westgate, Likens & Lindenmayer 2013). Understanding the spatio-temporal dynamics that underpin the distribution of animal populations within and across management zones, and how these are influenced by ecological and anthropogenic factors, is key to effective conservation planning (Hansen 2011; Delsink *et al.* 2013). Habitat quality is one factor affecting how animals interact with their environment (Pearson *et al.* 2011), and is a commonly explored theme in ecological studies (Turner, Gardner & O'Neill 2001; Battin 2004). High-quality habitats generally yield fitness benefits through increased opportunities for survival and reproduction, whereas low-quality habitats carry fitness costs due to increased mortality or reduced reproduction (Franklin *et al.* 2000; Delibes-Mateos, Ferreras & Gaona 2001). This conceptual framework forms the basis of source–sink theory (Pulliam 1988) and is considered a mechanistic foundation for landscape ecology (Wiens *et al.* 1993). Subsequent refinement of the source–sink model has enabled the inclusion of two essential concepts. First, habitats that exhibit relatively high survival due to the low risk of human-mediated mortality (Naves *et al.* 2003), but low reproduction due to suboptimal habitat, are considered 'refugia' (Stoner *et al.* 2013). In contrast, 'ecological traps' are characterized by high-quality habitat that exhibits reduced survival (Schlaepfer, Runge & Sherman 2002; Sánchez-Mercado *et al.* 2014), often due to human activity such as over-hunting or excessive retaliatory killing (Delibes-Mateos, Ferreras & Gaona 2001; Naves *et al.* 2003; Hansen 2011). These scenarios can lead to maladaptive habitat selection by animals, which may threaten their long-term persistence (Schlaepfer, Runge & Sherman 2002; Battin 2004; Gilroy & Sutherland 2007).

Identifying refugia and ecological traps is critical to enable conservation practitioners to focus resources in areas of concern (Naves *et al.* 2003; Stoner *et al.* 2013). Although a number of empirical studies have demonstrated the existence of such areas (e.g., Woodward et al. 2001, Weldon & Haddad 2005, van der Meer 2011), few have done so at the spatial scales required to inform management (Robertson & Hutto 2006). Scale mismatching (i.e., where the implementation of conservation research and actions do not reflect the scale of the conservation problem) occurs frequently in natural resource management, resulting in inefficiencies, a loss of system components, and failure to achieve management objectives (Cumming, Cumming & Redman 2006; Guerrero *et al.* 2013). Many of the problems arising in conservation are a consequence of the mismatch between the scale of the management intervention and the scale of the ecological processes being managed (Delsink *et al.* 2013).

The leopard (*Panthera pardus)* typifies the challenges faced in conservation. Leopards are the most widely distributed felid, occurring across much of sub-Saharan African, the Middle East and tropical Asia (Hunter, Henschel & Ray 2013). This extensive distribution, together with their wide-ranging movements, dictate that management of leopards occurs at large spatial scales. Despite their ubiquity, leopards are habitat selective (Balme, Hunter & Slotow 2007; Pitman *et al.* 2013a), which may lead to maladaptive behaviour in human affected landscapes. Like most large carnivores, leopards are frequently implicated in conflict centered around livestock and game depredation (Kissui 2008; Thorn *et al.* 2013), often leading to retaliatory killing of putative problem individuals (Hunter, Henschel & Ray 2013; Thorn *et al.* 2013). Leopards are also legally trophy hunted in many parts of Africa (Balme *et al.* 2010). Most range states lack science-based guidelines on how to effectively manage leopard hunting and problem animal control, particularly at the scales relevant to leopard conservation and that take into consideration the suitability of leopard habitat (Balme *et al.* 2014).

We use an approach previously applied to cougar (*Puma concolor)* (Stoner *et al.* 2013) to identify *de facto* refugia and ecological traps among leopard populations at multiple scales in Limpopo Province, South Africa. We use historical trophy hunting and problem leopard permit records to assess the relationship between human-mediated leopard mortality and habitat quality. Due to past ad-hoc regulation, we predict that the highest levels of offtake will be focused in the most suitable leopard habitat, likely leading to a predominance of ecological traps which may threaten the persistence of the wider provincial leopard population. We assess these relationships at three geographical scales using trophy hunting permits records alone, and then in combination with problem leopard permit records to (1) investigate the compounding effect of additional forms of offtake on leopard harvesting, and (2) to investigate the potential for management scale mismatching. Finally, we propose an adaptive, science-based regulatory framework aimed at improving leopard management practices in Limpopo, but which has broader applicability for the management of other large carnivores exposed to trophy hunting or population control.

## 2.3 METHODOLOGY

### 2.3.1 Study area

Limpopo (ca. 125 977 km$^2$; Fig. 2.1) represents the most suitable, contiguous leopard habitat across South Africa (Swanepoel *et al.* 2013), and is likely the most important province in South Africa for leopard conservation (Daly *et al.* 2005). To legally hunt a leopard, a person must be in possession of a trophy hunting permit issued by the Limpopo Department of Economic Development, Environment and Tourism (LEDET). The LEDET also award problem leopard permits, which are required by landowners for the removal of putative problem individuals. Limpopo award the most trophy hunting and problem leopard permits of any province in South Africa (Daly *et al.* 2005; Lindsey *et al.* 2011).

### 2.3.2 Sampling units and leopard offtake rates

Variation in leopard offtake rates were evaluated at three scales: (1) from a provincial district scale ($N$ = 5) representing the current administrative unit used by the LEDET to manage leopard, (2) from a municipal scale ($N$ = 25) which offers a finer and more intuitive administrative unit for management (Statistics South Africa 2011), and (3) from a quaternary catchment scale ($N$ = 194) on the premise that catchment zones provide a more ecologically meaningful management unit than municipalities or districts (South African Department of Agriculture, Forestry and Fisheries 2013). We excluded the Kruger National Park (Limpopo region = 9879 km$^2$) from all analyses since it is neither administered by the LEDET, nor open to leopard hunting or retaliatory killing (Fig. 2.1). All other ‘conservation areas’ were included in our analyses because many of these areas are open to leopard hunting or retaliatory killing and their small size (range: 1–1922 km$^2$) renders them vulnerable to edge effects (Balme, Slotow & Hunter 2010).

Data were compiled from trophy hunting (*N* = 354) and problem leopard (*N* = 403) permit records issued by the LEDET between January 2007 and December 2012 (*N* = 757; Fig. 2.1). In Limpopo, trophy hunted leopard are usually targeted using camera-traps at baited sites; whilst problem leopard are destroyed in an ad hoc fashion using gin traps, cages, poison or lured to baited sites where they are shot (LEDET, unpublished data). Leopard offtake rates were defined as the average number of leopard killed per year per 100 km$^2$ at all three scales. Unsuccessful hunts were removed from all analyses (*N* = 76). Mortality events were accurate to the property-level (Cadastral Spatial Information, Pretoria). Illegal hunting of leopard in Limpopo likely eclipses legal hunting (St John *et al.* 2012), but given the challenges in accurately monitoring these activities they could not be included in our analyses.

### 2.3.3 Habitat quality, de facto refugia and ecological traps

A map of leopard habitat suitability derived from maximum entropy-based (MaxEnt) habitat models was used as a predictor of habitat quality and potential leopard density (Swanepoel *et al.* 2013). Approximately 63% of Limpopo is considered suitable leopard habitat, which was grouped into four classes following Swanepoel et al. (2013): low quality (habitat suitability index = 0–0.22), medium quality (0.23–0.50), high quality (0.60–0.75), and very high quality (>0.75). Leopard densities were derived from Swanepoel et al. (Swanepoel *et al.* 2014a) such that low-, medium-, high- and very high-quality habitat were assigned population densities of 0.56 ± 0.02, 1.97 ± 0.12, 3.29 ± 0.14, and 3.81 ± 0.09 leopard per 100 km$^2$, respectively. These densities agreed with previous estimates for regional leopard population sizes in Limpopo (Norton 1990; Daly *et al.* 2005). Since sampling units often comprised >1 habitat class, leopard densities were multiplied by the area of each habitat class in each sampling unit to obtain an estimated leopard population size per sampling unit. Caro et al (2009) (Caro *et al.* 2009) used age-sex structured density independent models to determine maximum sustainable harvest for leopard; removal of ≤3.6% of the estimated population is considered sustainable for populations where both male and female leopard are hunted (Caro *et al.* 2009). Given that information on local context sustainability is not known, we set Limpopo's annual sustainable offtake to 3.6%, and used this value to categorically distinguish refugia (annual offtake rates ≤3.6%) from ecological traps (annual offtake rates >3.6%) following Stoner et al. (2013).

### 2.3.4 Statistical Analysis

Friedman tests were used to evaluate the distribution of leopard trophy hunts and problem leopard offtake at the district-scale from 2007–2012. A generalized linear model (GLM) based on a zero-inflated probability distribution was used to examine the effect of habitat quality on leopard offtake rates at all scales. A two-factor analysis of variance (ANOVA) with replication was used to assess the size of refugia and ecological traps at all scales. A single-factor ANOVA was used to assess the distances between 'spatially aggregated' refugia (i.e., refugia that only abut other refugia) and their closest ecological trap. The sizes of refugia and ecological traps, and Euclidean distances between refugia and ecological traps, were square-root transformed to meet assumptions of normality. All statistical analyses were conducted in R v.3.0.2 (R Core Team 2016). Spatial analyses were conducted in ArcGIS v.10.1 (ESRI, Redlands, USA). Unless otherwise stated, we present means with 95% confidence intervals (CI) as a measure of precision.

## 2.4 RESULTS

### 2.4.1 Leopard offtake rates

On average, 67 ± 2 leopard were trophy hunted each year in Limpopo, and 59 ± 3 were legally killed as putative problem animals. Problem leopard offtake differed significantly (FRIEDMAN: $\chi^2_6$ = 14.3, $P$ = 0.03; Fig. 2.2a) among districts from 2007 to 2012, whereas trophy hunting offtake approached significance (FRIEDMAN: $\chi^2_6$ = 12.1, $P$ = 0.06; Fig. 2.2a). The Waterberg district accounted for the vast majority (55%) of leopard mortality events, followed by Vhembe (21%), Capricorn (12%), Mopani (10%), and Sekhukhune (2%). Across all districts, total leopard offtake was greatest in 2010 ($N$ = 173) and 2012 ($N$ = 159). Problem leopard offtake was greatest in 2008 ($N$ = 87) and 2012 ($N$ = 92), while trophy hunting offtake peaked in 2009 ($N$ = 78), 2010 ($N$ = 93) and 2012 ($N$ = 67).

### 2.4.2 Habitat quality and mortality risk

According to the MaxEnt habitat model, Limpopo comprised 36% low-quality habitat, 45% medium-quality habitat, 15% high-quality habitat, 1% very high-quality habitat, and 3% undefined habitat (due to missing data; Swanepoel et al. 2013). Leopard offtake rates were significantly affected by habitat quality at the catchment-scale (zero-inflated GLM: trophy hunting scenario: $z = -3.60$, $P < 0.001$; trophy hunting and problem leopard scenario: $z = -3.98$, $P < 0.001$) and municipal-scale (zero-inflated GLM: trophy hunting scenario: $z = -4.17$, $P < 0.001$; trophy hunting and problem leopard scenario: $z = -3.78$, $P < 0.001$), but not at the district-scale (zero-inflated GLM: trophy hunting scenario: $z = -0.01$, $P > 0.5$; trophy hunting and problem leopard scenario: $z = -0.01$, $P > 0.5$).

### 2.4.3 De facto refugia and ecological traps

When determining refugia and ecological traps using trophy hunting permits alone, the total area of refugia at a catchment (74 556 km$^2$, $N = 145$) and a municipal (70 847 km$^2$, $N = 19$) scale exceeded that of ecological traps (catchment = 41 519 km$^2$, $N = 48$; municipality = 45 210 km$^2$, $N = 6$) by 44% and 36%, respectively (Supporting Information 1; Fig. 2.2b). In contrast, the total area of ecological traps (80 773 km$^2$, $N = 3$) at the district-scale exceeded refugia (35 282 km$^2$, $N = 2$) by 56% (Supporting Information 1; Fig. 2.2b). Refugia (catchment = 514 km$^2$; municipality = 3729 km$^2$, district = 17 641 km$^2$) were significantly smaller than ecological traps (catchment = 865 km$^2$; municipality = 7535 km$^2$, district = 26 924 km$^2$; ANOVA: $F_{2,\,217} = 5.96$, $P = 0.003$) at all scales. Mean annual offtake rates within ecological traps were 94% (catchment-scale), 83% (municipal-scale) and 66% (district-scale) greater than in refugia (Fig. 2.2c). A total of 73 (50%), 12 (63%), and 2 (100%) refugia abutted an ecological trap from a catchment-, municipal- and district-scale, respectively (Fig. 2.3 A–C). The distances between the remaining 'spatially aggregated' refugia and their closest ecological trap were significantly different (ANOVA: $F_{1,\,77} = 6.79$, $P < 0.05$) at the catchment- (21 ± 0.82 km) and municipal-scale (41 ± 3.36 km; Fig. 2.3 A–C). A district-scale approach to management would misclassify (i.e., classify an area as a refuge when it should be classified as an ecological trap; and vice versa) 5531 km$^2$ of refugia and 44 797 km$^2$ of ecological traps when measured against the catchment-scale; similarly, a municipal-scale approach to management would misclassify 12 606 km$^2$ of refugia and 16 306 km$^2$ of ecological traps when measured against the catchment-scale. Using trophy hunting permits alone, offtake within ecological traps exceeded what is considered sustainable (Caro *et al.* 2009) by up to 19.07% (offtake range per annum: 3.63-22.67%), 7.32% (offtake range per annum: 3.71-10.92%), and 2.32% (offtake range per annum: 3.63-5.92%) from a catchment-, municipal-, and district-scale, respectively (Supporting Information 1).

When determining refugia and ecological traps using a combination of trophy hunting and problem leopard permits, the total area of ecological traps (catchment = 71 212 km$^2$, $N$ = 84; municipality = 79 588 km$^2$, $N$ = 12; district = 102 504 km$^2$, $N$ = 4; Supporting Information 1) exceeded that of refugia (catchment = 44 863 km$^2$, $N$ = 109; municipality = 36 469 km$^2$, $N$ = 13; district = 13 551 km$^2$, $N$ = 1; Supporting Information 1) from a catchment-, municipal- and district-scale by 37%, 54% and 87%, respectively (Fig. 2.2b). Refugia (catchment = 412 km$^2$; municipality = 2805 km$^2$, district = 13 551 km$^2$) were significantly smaller than ecological traps (catchment = 848 km$^2$; municipality = 6632 km$^2$, district = 25 626 km$^2$; ANOVA: $F_{2, 217} = 10.07$, $P < 0.001$) at all scales. Mean annual offtake rates within ecological traps were 96% (catchment-scale), 86% (municipal-scale) and 80% (district-scale) greater than in refugia (Fig. 2.2c). A total of 68 (62%), 10 (77%), and 1 (100%) refugia abutted an ecological trap from a catchment-, municipal- and district-scale, respectively (Fig. 2.3 D–F). There was no significant difference (ANOVA: $F_{1, 42} = 0.01$, $P = 0.9$) in the distances between the remaining 'spatially aggregated' refugia and their closest ecological trap at the catchment- (14 ± 0.76 km) and municipal-scale (12 ± 2.27 km; Fig. 2.3 D – F). A district-scale approach to management would misclassify 2539 km$^2$ of refugia and 33 847 km$^2$ of ecological traps when measured against the catchment-scale; similarly, a municipal-scale approach to management would misclassify 8325 km$^2$ of refugia and 16 713 km$^2$ of ecological traps when measured against the catchment-scale. Using trophy hunting and problem leopard permits, offtake within ecological traps exceeded what is considered sustainable (Caro *et al.* 2009) by up to 61.87% (offtake range per annum: 3.63-65.47%), 10.82% (offtake range per annum: 4.51-14.42%), and 6.80% (offtake range per annum: 6.22-10.40%) from a catchment-, municipal-, and district-scale, respectively (Supporting Information 1).

## 2.5 DISCUSSION

In many developing countries, conservation authorities lack the human and financial resources to accurately and consistently monitor wildlife populations (Rodríguez *et al.* 2005), particularly cryptic species such as leopard that range widely, and occur mainly outside of formally protected areas (Swanepoel *et al.* 2013). As a result, carnivore management is rarely underpinned by strong science (Ray, Hunter & Zigouris 2005). Here, we demonstrate a rigorous approach for identifying *de facto* refugia and ecological traps among leopard populations at multiple scales, which can be readily incorporated in a management framework without requiring detailed knowledge of local animal numbers or movements. Such an approach enables authorities to quantitatively evaluate the impact of human-mediated mortality and implement management interventions by using data that are easily and cheaply sourced. A similar model was previously proposed to manage cougar harvest in North America (Stoner *et al.* 2013), and it appears equally suitable for regulating the hunting of leopard in Limpopo.

In Limpopo, human-mediated leopard mortality was greatest in prime leopard habitat. Leopard are capable of distinguishing and selecting high-quality habitats (Balme, Hunter & Slotow 2007; Pitman *et al.* 2013a), a trait which is likely maladaptive in Limpopo due to the fitness costs associated with such habitat (Delibes-Mateos, Ferreras & Gaona 2001). African wild dogs *(Lycoan pictus)* in Hwange National Park, Zimbabwe, similarly selected high-quality habitat within the buffer zone of the protected area, thereby increasing their risk of human-induced mortality (van der Meer *et al.* 2014). Localized population densities may be maintained in ecological traps by immigration from adjacent suboptimal habitat (Gilroy & Sutherland 2007), even as the broader metapopulation declines (Battin 2004). For example, closed population models predicted a precipitous decline of a heavily hunted cougar population within prime cougar habitat, whilst the population actually remained stable due to increased immigration from nearby refugia (Robinson *et al.* 2008). Such compensatory immigration may erroneously suggest wider population stability or even growth, often leading to increased public pressure to maintain or raise harvest levels (Cooley *et al.* 2009). These scenarios are difficult to detect *in situ* and may ultimately cause the local extirpation of animal populations (Cooley 2008; Robinson *et al.* 2008).

Compensatory immigration is partly dependent on the distribution of refugia in relation to ecological traps. The majority of Limpopo's refugia abut an ecological trap, which puts supposedly safe leopard populations in close proximity to elevated sources of human-mediated mortality. The negative consequences of this were demonstrated in KwaZulu-Natal Province, South Africa, where leopard within a protected area experienced higher levels of human-mediated mortality the closer they ventured to the reserve boundary (Balme, Slotow & Hunter 2010). Although 'spatially aggregated' refugia have a reduced risk of mortality

(Sánchez-Mercado *et al.* 2014), in Limpopo, these areas are still within dispersal distance (catchment: 14–21 km; municipality: 12–41 km) of ecological traps for leopard (Fattebert *et al.* 2013). Fattebert et al. (Fattebert *et al.* 2015) demonstrated that dispersing subadult leopard favour suitable habitat. Given that habitat selection by leopard in Limpopo is likely maladaptive, further concern is raised regarding the success of dispersal from, and within, refugia and ecological traps. Increased connectivity is typically beneficial for population persistence (Rabinowitz & Zeller 2010), but it may be detrimental in the context of managing the wider impacts of ecological traps. These negative consequences are further exacerbated when we consider that refugia across Limpopo are significantly smaller, with lower habitat suitability, lower leopard densities, and greater human population densities, than ecological traps. Although this may suggest that refugia offer little conservation value, research on cougar suggest that, in the event of widespread human-mediated mortality, refugia are likely to harbor carnivore populations and may therefore have greater conservation value than previously assumed (Stoner *et al.* 2013).

The relative size and distribution of refugia to ecological traps suggest that leopard management practices in Limpopo may not be sustainable when based on a maximum sustainable offtake rate of ≤3.6 % (Caro et al. 2009; see Stoner et al. 2013). Historically, the LEDET has not quantified and included problem leopard offtake when administering trophy hunting permits. Similar to research on gray wolf (Creel & Rotella 2010), our study emphasizes the importance of considering the compounding effects of other forms of human-mediated mortality when evaluating the impact of harvesting. Limpopo currently issues three-times more problem leopard permits per year than any other province in South Africa (Lindsey *et al.* 2011). Problem leopard complaints are almost exclusively attributed to livestock and game depredation (LEDET unpublished data). To appropriately deal with the issue of problem animal control, conservation authorities require official guidelines on how to manage problem animals (see Balme et al. 2009). Furthermore, landowners can be encouraged to implement a variety of traditional and modern non-lethal techniques to reduce the risk of stock depredation (Stahl *et al.* 2002; Ogada *et al.* 2003; Marker & Dickman 2005). By our estimates, Limpopo's current offtake is well beyond what Caro et al. (2009) would indicate is sustainable. However, a better understanding of population demographics within the local context is needed in order to define sustainable offtake in Limpopo. This will require more detailed population information, as well as demographic modelling for defining sustainability under the local context—similar to research on elephant (*Loxodonta africana)* subject to hunting and problem animal control in north-western Limpopo (Selier *et al.* 2014). Illegal offtake of carnivores in South Africa's Northern provinces are greater than levels of legal offtake (St John *et al.* 2012; Thorn *et al.* 2013) indicating that our results are conservative since we could not account for illegal killing of leopard. Conservation authorities should either attempt to include some estimate of annual illegal offtake (perhaps through innovative questionnaire-based methods; see St John et al. 2012), or apply conservative annual quotas since mortality rates are likely underestimated.

Scaling issues are beginning to feature prominently in conservation planning, for instance, Delsink et al. (2013) demonstrated how current management zones for African elephant in Kruger National Park are not biologically relevant or appropriate for elephant management. In Limpopo, leopard trophy hunting is currently managed at the district-scale; however, this level of management is too coarse and unable to detect the maladaptive relationship between leopard mortality and habitat quality. A district-scale approach to management consistently misclassifies large areas of refugia and ecological traps, regardless of whether problem leopard control is taken into account. Allocating leopard trophy hunting permits across a finer-scaled management unit will (1) facilitate a more evenly distributed harvest, (2) allow conservation authorities to pinpoint potential areas of over-utilization, (3) benefit landowners that have previously not had an opportunity to host a leopard hunt, and (4) preserve or restore the integrity of leopard population structure by the creation of fewer ecological traps. Even though a municipal-scale approach to management would misclassify a smaller area of refugia and ecological traps when compared to the district-scale, a catchment-scale approach to management remains the most precise at identifying areas of potentially unsustainable offtake.

Our study highlights the importance of identifying *de facto* refugia and ecological traps, management scale mismatching, and the worrying relationship between disproportionately high human-mediated leopard mortality in prime habitat when devising leopard management policies. To counter these challenges, we recommend an adaptive, science-based approach to leopard management; specifically: (1) shift leopard management to a smaller scale, (2) account for problem leopard offtake in the determination of annual hunting quotas, (3) undertake a local context specific modelling exercise on an annual basis to better define the level of sustainable offtake, and (4) use this sustainable offtake rate to identify and reduce the number of ecological traps. These recommendations fall within the capacity South African conservation authorities and potentially more widely. A similar management approach that accounts for refugia and ecological traps could readily be applied to other wide-ranging species that undergo harvest or population control.

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## 2.7 SUPPORTING INFORMATION

Supporting Information 2.1. Characteristics of catchments (*N* = 194), municipalities (*N* = 25) and districts (*N* = 5) across Limpopo Province, South Africa.

| | | | | | | | Trophy Hunting | | | Trophy Hunting & Problem Leopard Control | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Management Zone | Problem Leopard Control[A] | Trophy Hunting[A] | Area ($km^2$) | Human Population Density ($km^2$)[B] | Habitat Quality | Category | Offtake Rate Per Annum (%) | Leopards[C] | Category | Offtake Rate Per Annum (%) | Leopards[C] |
| Catchments | A24E | 2 | 0 | 195 | 20 | Low | Refuge | 0 | 0 | Ecological Trap | 29.13 | -0.35 |
| | A61G | 1 | 0 | 928 | 98 | Low | Refuge | 0 | 0.4 | Refuge | 1.73 | 0.22 |
| | B31J | 1 | 1 | 1 352 | 40 | Low | Refuge | 1.28 | 0.4 | Refuge | 2.56 | 0.16 |
| | B41B | 0 | 0 | 95 | 19 | Low | Refuge | 0 | 0 | Refuge | 0 | 0.02 |
| | A23C | 0 | 0 | 403 | 10 | Low | Refuge | 0 | 0.2 | Refuge | 0 | 0.16 |
| | A71B | 0 | 0 | 884 | 191 | Low | Refuge | 0 | 0.2 | Refuge | 0 | 0.19 |
| | B41C | 0 | 0 | 285 | 18 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.11 |
| | B81H | 0 | 0 | 670 | 68 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.14 |
| | A23G | 0 | 0 | 767 | 63 | Low | Refuge | 0 | 0.3 | Refuge | 0 | 0.28 |
| | A71E | 0 | 1 | 894 | 92 | Low | Refuge | 3.09 | 0 | Refuge | 3.09 | 0.03 |
| | A71A | 0 | 0 | 1 146 | 199 | Low | Refuge | 0 | 0.3 | Refuge | 0 | 0.34 |
| | B51E | 9 | 1 | 2 930 | 22 | Low | Refuge | 0.66 | 0.9 | Ecological Trap | 6.56 | -0.9 |
| | A72A | 2 | 1 | 1 910 | 48 | Low | Refuge | 0.84 | 0.7 | Refuge | 2.53 | 0.25 |
| | B51C | 1 | 0 | 639 | 61 | Low | Refuge | 0 | 0.2 | Ecological Trap | 4.3 | -0.03 |
| | B31E | 1 | 1 | 974 | 10 | Low | Refuge | 3.08 | 0 | Ecological Trap | 6.15 | -0.17 |
| | A24D | 0 | 0 | 86 | 15 | Low | Refuge | 0 | 0 | Refuge | 0 | 0.02 |
| | B31F | 0 | 0 | 33 | 65 | Low | Refuge | 0 | 0 | Refuge | 0 | 0 |
| | B32E | 0 | 0 | 195 | 8 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.07 |
| | B51A | 0 | 0 | 312 | 147 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.06 |
| | B52C | 0 | 0 | 201 | 23 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.05 |
| | B52D | 0 | 0 | 342 | 176 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.08 |
| | B52F | 0 | 0 | 119 | 72 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.07 |
| | B72G | 0 | 0 | 48 | 50 | Low | Refuge | 0 | 0 | Refuge | 0 | 0.03 |
| | B90C | 0 | 0 | 246 | 121 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.05 |
| | A62E | 0 | 0 | 621 | 75 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.14 |
| | A91G | 0 | 0 | 407 | 271 | Low | Refuge | 0 | 0.2 | Refuge | 0 | 0.17 |
| | A92A | 0 | 0 | 330 | 145 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.14 |
| | A92C | 0 | 0 | 456 | 54 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.13 |
| | B31H | 0 | 0 | 402 | 103 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.11 |
| | B32J | 0 | 0 | 323 | 174 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.14 |
| | B51G | 0 | 0 | 592 | 111 | Low | Refuge | 0 | 0.2 | Refuge | 0 | 0.17 |
| | B51H | 0 | 0 | 719 | 168 | Low | Refuge | 0 | 0.2 | Refuge | 0 | 0.15 |
| | B52B | 0 | 0 | 634 | 134 | Low | Refuge | 0 | 0.2 | Refuge | 0 | 0.18 |
| | B81G | 0 | 0 | 514 | 198 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.13 |
| | B82H | 0 | 0 | 746 | 91 | Low | Refuge | 0 | 0.2 | Refuge | 0 | 0.18 |
| | B90B | 0 | 0 | 358 | 109 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.11 |
| | B90F | 0 | 0 | 425 | 102 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.1 |
| | A62F | 0 | 0 | 620 | 51 | Low | Refuge | 0 | 0.3 | Refuge | 0 | 0.29 |
| | A62H | 0 | 0 | 872 | 52 | Low | Refuge | 0 | 0.2 | Refuge | 0 | 0.23 |
| | A91F | 0 | 0 | 582 | 213 | Low | Refuge | 0 | 0.2 | Refuge | 0 | 0.2 |
| | B52H | 0 | 0 | 564 | 127 | Low | Refuge | 0 | 0.2 | Refuge | 0 | 0.2 |
| | B71E | 0 | 0 | 784 | 122 | Low | Refuge | 0 | 0.3 | Refuge | 0 | 0.29 |
| | A71F | 1 | 1 | 684 | 86 | Low | Refuge | 3.51 | 0 | Ecological Trap | 7.03 | -0.2 |
| | B51B | 1 | 0 | 592 | 77 | Low | Refuge | 0 | 0.3 | Refuge | 2.87 | 0.05 |
| | A91E | 0 | 0 | 224 | 566 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.08 |
| | B90G | 0 | 0 | 15 | 9 | Low | Refuge | 0 | 0 | Refuge | 0 | 0 |
| | B52A | 0 | 0 | 567 | 76 | Low | Refuge | 0 | 0.1 | Refuge | 0 | 0.13 |
| | B32G | 0 | 0 | 100 | 306 | Low | Refuge | 0 | 0 | Refuge | 0 | 0.02 |
| | B82F | 0 | 1 | 762 | 176 | Low | Refuge | 3.22 | 0 | Refuge | 3.22 | 0.02 |
| | B82D | 2 | 2 | 633 | 134 | Low | Ecological Trap | 8.08 | -0.2 | Ecological Trap | 16.16 | -0.62 |
| | B60F | 1 | 1 | 159 | 11 | Low | Ecological Trap | 11.42 | -0.1 | Ecological Trap | 22.85 | -0.34 |
| | A41D | 17 | 5 | 1 911 | 1 | Low | Ecological Trap | 6.25 | -0.4 | Ecological Trap | 27.49 | -3.82 |
| | A63E | 1 | 17 | 1 990 | 3 | Low | Ecological Trap | 17.24 | -2.7 | Ecological Trap | 18.26 | -2.89 |
| | B81A | 0 | 1 | 169 | 26 | Low | Ecological Trap | 16.16 | -0.2 | Ecological Trap | 16.16 | -0.16 |
| | B82G | 0 | 1 | 923 | 112 | Low | Ecological Trap | 3.63 | 0 | Ecological Trap | 3.63 | 0 |
| | A71C | 0 | 3 | 1 333 | 59 | Low | Ecological Trap | 4.15 | -0.1 | Ecological Trap | 4.15 | -0.08 |
| | A24J | 21 | 6 | 2 417 | 3 | Medium | Refuge | 2.95 | 0.3 | Ecological Trap | 13.3 | -3.94 |
| | A80E | 6 | 0 | 248 | 54 | Medium | Refuge | 0 | 0.2 | Ecological Trap | 18.55 | -0.97 |
| | A61F | 6 | 1 | 790 | 128 | Medium | Refuge | 1.89 | 0.2 | Ecological Trap | 13.26 | -1.02 |
| | B72H | 4 | 1 | 387 | 19 | Medium | Refuge | 2.17 | 0.1 | Ecological Trap | 10.85 | -0.67 |
| | B81J | 4 | 0 | 569 | 28 | Medium | Refuge | 0 | 0.3 | Ecological Trap | 8.52 | -0.46 |
| | A42D | 2 | 1 | 497 | 2 | Medium | Refuge | 1.61 | 0.2 | Ecological Trap | 4.83 | -0.15 |
| | B60J | 2 | 1 | 617 | 11 | Medium | Refuge | 1.52 | 0.3 | Ecological Trap | 4.57 | -0.13 |
| | A61A | 1 | 0 | 382 | 81 | Medium | Refuge | 0 | 0.3 | Refuge | 2.53 | 0.08 |
| | B82E | 1 | 1 | 424 | 47 | Medium | Refuge | 3.15 | 0 | Ecological Trap | 6.29 | -0.17 |
| | B83A | 1 | 0 | 227 | 37 | Medium | Refuge | 0 | 0.2 | Refuge | 3.41 | 0.01 |
| | A62J | 1 | 3 | 930 | 18 | Medium | Refuge | 3.23 | 0.1 | Ecological Trap | 4.3 | -0.13 |
| | B32B | 0 | 0 | 12 | 8 | Medium | Refuge | 0 | 0 | Refuge | 0 | 0.01 |
| | B41F | 0 | 0 | 96 | 9 | Medium | Refuge | 0 | 0.1 | Refuge | 0 | 0.06 |
| | A80A | 0 | 0 | 288 | 153 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.19 |
| | B72E | 0 | 0 | 321 | 109 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.19 |
| | A62C | 0 | 0 | 385 | 32 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.23 |
| | A91B | 0 | 0 | 275 | 46 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.22 |
| | B41H | 0 | 0 | 400 | 104 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.21 |
| | B52G | 0 | 0 | 291 | 73 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.21 |
| | B71A | 0 | 0 | 298 | 17 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.23 |
| | B71B | 0 | 0 | 275 | 37 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.23 |
| | B71H | 0 | 0 | 331 | 48 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.22 |
| | A92B | 0 | 0 | 567 | 77 | Medium | Refuge | 0 | 0.3 | Refuge | 0 | 0.32 |
| | B72A | 0 | 1 | 536 | 97 | Medium | Refuge | 2.18 | 0.1 | Refuge | 2.18 | 0.13 |
| | B81D | 0 | 0 | 480 | 267 | Medium | Refuge | 0 | 0.3 | Refuge | 0 | 0.3 |
| | A24H | 14 | 4 | 1 338 | 24 | Medium | Refuge | 2.84 | 0.2 | Ecological Trap | 12.8 | -2.59 |
| | A23H | 8 | 0 | 805 | 6 | Medium | Refuge | 0 | 0.4 | Ecological Trap | 13.14 | -1.16 |
| | A80D | 7 | 0 | 128 | 7 | Medium | Refuge | 0 | 0.1 | Ecological Trap | 53.84 | -1.31 |
| | A32E | 7 | 6 | 2 374 | 1 | Medium | Refuge | 2.84 | 0.3 | Ecological Trap | 6.15 | -1.08 |
| | B72K | 5 | 3 | 970 | 114 | Medium | Refuge | 3.03 | 0.1 | Ecological Trap | 8.08 | -0.89 |
| | A63B | 5 | 2 | 1 506 | 18 | Medium | Refuge | 1.61 | 0.5 | Ecological Trap | 5.64 | -0.51 |
| | B82B | 4 | 0 | 407 | 31 | Medium | Refuge | 0 | 0.3 | Ecological Trap | 10.38 | -0.52 |
| | B60G | 4 | 0 | 372 | 12 | Medium | Refuge | 0 | 0.3 | Ecological Trap | 9.57 | -0.5 |
| | A71G | 4 | 2 | 876 | 32 | Medium | Refuge | 2.83 | 0.1 | Ecological Trap | 8.5 | -0.69 |
| | B81F | 3 | 0 | 1 204 | 73 | Medium | Refuge | 0 | 0.6 | Ecological Trap | 3.69 | -0.01 |
| | A42E | 3 | 0 | 1 008 | 11 | Medium | Refuge | 0 | 0.8 | Refuge | 2.7 | 0.2 |
| | A72B | 3 | 5 | 1 557 | 6 | Medium | Refuge | 2.76 | 0.3 | Ecological Trap | 4.41 | -0.29 |
| | B32F | 2 | 0 | 668 | 42 | Medium | Refuge | 0 | 0.3 | Ecological Trap | 4.87 | -0.1 |
| | A24B | 2 | 0 | 564 | 8 | Medium | Refuge | 0 | 0.3 | Ecological Trap | 4.31 | -0.07 |
| | A24F | 2 | 1 | 591 | 34 | Medium | Refuge | 2.34 | 0.1 | Ecological Trap | 7.01 | -0.29 |
| | A61C | 2 | 0 | 587 | 13 | Medium | Refuge | 0 | 0.3 | Ecological Trap | 4.21 | -0.06 |
| | A42B | 2 | 2 | 522 | 3 | Medium | Refuge | 3.18 | 0.1 | Ecological Trap | 6.35 | -0.35 |
| | A62B | 2 | 0 | 711 | 39 | Medium | Refuge | 0 | 0.5 | Refuge | 2.87 | 0.1 |
| | A80J | 2 | 1 | 869 | 22 | Medium | Refuge | 1.25 | 0.4 | Ecological Trap | 3.75 | -0.02 |
| | B73A | 1 | 0 | 37 | 9 | Medium | Refuge | 0 | 0 | Ecological Trap | 65.47 | -0.19 |
| | A61D | 1 | 1 | 456 | 31 | Medium | Refuge | 2.93 | 0 | Ecological Trap | 5.86 | -0.15 |
| | A62G | 1 | 1 | 627 | 28 | Medium | Refuge | 1.88 | 0.2 | Ecological Trap | 3.76 | -0.02 |
| | B42H | 1 | 0 | 392 | 18 | Medium | Refuge | 0 | 0.3 | Refuge | 2.27 | 0.12 |
| | B41J | 1 | 0 | 688 | 126 | Medium | Refuge | 0 | 0.5 | Refuge | 1.48 | 0.29 |
| | A63A | 1 | 4 | 1 929 | 11 | Medium | Refuge | 2.07 | 0.6 | Refuge | 2.59 | 0.39 |
| | A91D | 0 | 0 | 133 | 173 | Medium | Refuge | 0 | 0.1 | Refuge | 0 | 0.08 |
| | B42G | 0 | 0 | 45 | 9 | Medium | Refuge | 0 | 0 | Refuge | 0 | 0.03 |
| | B73C | 0 | 0 | 32 | 75 | Medium | Refuge | 0 | 0 | Refuge | 0 | 0.02 |
| | B81C | 0 | 0 | 209 | 194 | Medium | Refuge | 0 | 0.1 | Refuge | 0 | 0.1 |
| | B90A | 0 | 0 | 30 | 137 | Medium | Refuge | 0 | 0 | Refuge | 0 | 0.03 |
| | A80H | 0 | 0 | 266 | 40 | Medium | Refuge | 0 | 0.1 | Refuge | 0 | 0.13 |
| | A91C | 0 | 0 | 250 | 137 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.15 |
| | B31D | 0 | 0 | 168 | 8 | Medium | Refuge | 0 | 0.1 | Refuge | 0 | 0.12 |
| | B41E | 0 | 0 | 238 | 66 | Medium | Refuge | 0 | 0.1 | Refuge | 0 | 0.13 |
| | B41G | 0 | 0 | 238 | 9 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.18 |
| | B51F | 0 | 0 | 395 | 10 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.19 |
| | B52E | 0 | 0 | 452 | 87 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.19 |
| | B82C | 0 | 0 | 300 | 85 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | 0.19 |
| | B72B | 0 | 1 | 333 | 11 | Medium | Refuge | 2.59 | 0.1 | Refuge | 2.59 | 0.08 |
| | B81B | 0 | 0 | 482 | 32 | Medium | Refuge | 0 | 0.3 | Refuge | 0 | 0.27 |
| | A41B | 0 | 1 | 357 | 1 | Medium | Refuge | 2.22 | 0.1 | Refuge | 2.22 | 0.12 |
| | A92D | 0 | 0 | 781 | 21 | Medium | Refuge | 0 | 0.3 | Refuge | 0 | 0.33 |
| | B32D | 0 | 0 | 522 | 20 | Medium | Refuge | 0 | 0.4 | Refuge | 0 | 0.37 |
| | B52J | 0 | 0 | 396 | 61 | Medium | Refuge | 0 | 0.3 | Refuge | 0 | 0.31 |
| | B41K | 0 | 0 | 637 | 92 | Medium | Refuge | 0 | 0.4 | Refuge | 0 | 0.44 |
| | B82A | 1 | 0 | 468 | 73 | Medium | Refuge | 0 | 0.3 | Refuge | 2.08 | 0.15 |
| | B31C | 0 | 0 | 116 | 8 | Medium | Refuge | 0 | 0.1 | Refuge | 0 | 0.1 |
| | B71J | 0 | 0 | 79 | 34 | Medium | Refuge | 0 | 0.1 | Refuge | 0 | 0.06 |
| | B32C | 0 | 0 | 192 | 8 | Medium | Refuge | 0 | 0.1 | Refuge | 0 | 0.12 |
| | B82J | 0 | 0 | 247 | 23 | Medium | Refuge | 0 | 0.1 | Refuge | 0 | 0.12 |
| | A91H | 0 | 0 | 429 | 134 | Medium | Refuge | 0 | 0.3 | Refuge | 0 | 0.27 |
| | B60H | 0 | 0 | 307 | 41 | Medium | Refuge | 0 | 0.2 | Refuge | 0 | NA |
| | A61E | 0 | 0 | 548 | 9 | Medium | Refuge | 0 | 0.3 | Refuge | 0 | 0.31 |
| | B32H | 0 | 0 | 599 | 70 | Medium | Refuge | 0 | 0.3 | Refuge | 0 | 0.32 |
| | A61H | 0 | 1 | 586 | 5 | Medium | Refuge | 1.61 | 0.2 | Refuge | 1.61 | 0.25 |
| | A63D | 6 | 7 | 1 320 | 11 | Medium | Ecological Trap | 6.38 | -0.6 | Ecological Trap | 11.85 | -1.81 |
| | A50A | 4 | 2 | 298 | 6 | Medium | Ecological Trap | 5.64 | -0.1 | Ecological Trap | 16.93 | -0.94 |
| | A24C | 3 | 4 | 765 | 15 | Medium | Ecological Trap | 7.84 | -0.4 | Ecological Trap | 13.72 | -1.03 |
| | A71J | 3 | 12 | 1 164 | 7 | Medium | Ecological Trap | 8.45 | -1.4 | Ecological Trap | 10.57 | -1.98 |
| | A61B | 2 | 3 | 363 | 24 | Medium | Ecological Trap | 9.6 | -0.4 | Ecological Trap | 15.99 | -0.77 |
| | B81E | 2 | 2 | 667 | 116 | Medium | Ecological Trap | 4.08 | 0 | Ecological Trap | 8.16 | -0.45 |
| | A42C | 2 | 5 | 699 | 8 | Medium | Ecological Trap | 7.95 | -0.5 | Ecological Trap | 11.13 | -0.95 |
| | A50G | 2 | 9 | 821 | 25 | Medium | Ecological Trap | 13.88 | -1.3 | Ecological Trap | 16.97 | -1.73 |
| | B72J | 2 | 10 | 539 | 13 | Medium | Ecological Trap | 16.17 | -1.6 | Ecological Trap | 19.4 | -1.95 |
| | A41A | 2 | 4 | 692 | 2 | Medium | Ecological Trap | 4.87 | -0.2 | Ecological Trap | 7.31 | -0.61 |
| | B73B | 1 | 2 | 316 | 6 | Medium | Ecological Trap | 5.9 | -0.2 | Ecological Trap | 8.86 | -0.36 |
| | A80C | 0 | 2 | 294 | 68 | Medium | Ecological Trap | 5.59 | -0.1 | Ecological Trap | 5.59 | -0.14 |
| | A63C | 21 | 20 | 1 318 | 2 | Medium | Ecological Trap | 22.67 | -3.4 | Ecological Trap | 46.47 | -7.56 |
| | A41E | 17 | 9 | 1 927 | 4 | Medium | Ecological Trap | 7.54 | -0.9 | Ecological Trap | 21.8 | -4.34 |
| | A42J | 13 | 9 | 1 811 | 16 | Medium | Ecological Trap | 4.99 | -0.5 | Ecological Trap | 12.19 | -3.1 |
| | A50J | 12 | 4 | 1 254 | 4 | Medium | Ecological Trap | 3.74 | 0 | Ecological Trap | 14.97 | -2.43 |
| | A71L | 11 | 14 | 1 762 | 2 | Medium | Ecological Trap | 14.44 | -2.1 | Ecological Trap | 25.78 | -4.3 |
| | A62A | 10 | 2 | 428 | 20 | Medium | Ecological Trap | 4.42 | -0.1 | Ecological Trap | 26.54 | -2.07 |
| | A41C | 10 | 8 | 1 111 | 1 | Medium | Ecological Trap | 6.68 | -0.7 | Ecological Trap | 15.02 | -2.74 |
| | A50E | 9 | 6 | 629 | 3 | Medium | Ecological Trap | 7.5 | -0.6 | Ecological Trap | 18.76 | -2.42 |
| | A50H | 9 | 5 | 1 943 | 15 | Medium | Ecological Trap | 4.06 | -0.1 | Ecological Trap | 11.37 | -1.91 |
| | A91A | 3 | 1 | 233 | 47 | Medium | Ecological Trap | 4.42 | 0 | Ecological Trap | 17.66 | -0.64 |
| | A80F | 3 | 4 | 631 | 9 | Medium | Ecological Trap | 5.27 | -0.3 | Ecological Trap | 9.23 | -0.85 |
| | A61J | 3 | 4 | 818 | 17 | Medium | Ecological Trap | 4.62 | -0.2 | Ecological Trap | 8.09 | -0.78 |
| | A71K | 3 | 8 | 1 672 | 20 | Medium | Ecological Trap | 4.18 | -0.2 | Ecological Trap | 5.75 | -0.82 |
| | A71D | 2 | 3 | 893 | 11 | Medium | Ecological Trap | 3.99 | -0.1 | Ecological Trap | 6.65 | -0.46 |
| | B72D | 2 | 12 | 856 | 8 | Medium | Ecological Trap | 11.01 | -1.6 | Ecological Trap | 12.84 | -2.02 |
| | A80G | 2 | 21 | 1 230 | 8 | Medium | Ecological Trap | 15.71 | -3.2 | Ecological Trap | 17.2 | -3.64 |
| | B72C | 1 | 5 | 336 | 23 | Medium | Ecological Trap | 16.34 | -0.8 | Ecological Trap | 19.61 | -0.98 |
| | A62D | 1 | 4 | 603 | 15 | Medium | Ecological Trap | 6.36 | -0.3 | Ecological Trap | 7.95 | -0.55 |
| | B73E | 0 | 1 | 107 | 6 | Medium | Ecological Trap | 9.93 | -0.1 | Ecological Trap | 9.93 | -0.13 |
| | A80B | 0 | 1 | 252 | 195 | Medium | Ecological Trap | 4.16 | 0 | Ecological Trap | 4.16 | -0.03 |
| | B41D | 0 | 1 | 404 | 42 | Medium | Ecological Trap | 3.66 | 0 | Ecological Trap | 3.66 | 0 |
| | A71H | 0 | 8 | 1 014 | 70 | Medium | Ecological Trap | 8.34 | -0.9 | Ecological Trap | 8.34 | -0.91 |
| | A42A | 1 | 4 | 574 | 9 | Medium | Ecological Trap | 6.89 | -0.4 | Ecological Trap | 8.61 | -0.58 |
| | A91J | 0 | 0 | 162 | 38 | High | Refuge | 0 | 0.2 | Refuge | 0 | 0.17 |
| | B71D | 0 | 0 | 228 | 24 | High | Refuge | 0 | 0.2 | Refuge | 0 | 0.23 |
| | A24G | 8 | 2 | 735 | 5 | High | Refuge | 2.06 | 0.3 | Ecological Trap | 10.31 | -1.3 |
| | A32D | 1 | 0 | 199 | 1 | High | Refuge | 0 | 0.2 | Ecological Trap | 3.74 | -0.01 |
| | A50B | 1 | 1 | 407 | 4 | High | Refuge | 1.54 | 0.3 | Refuge | 3.09 | 0.07 |
| | B71F | 1 | 0 | 542 | 40 | High | Refuge | 0 | 0.6 | Refuge | 1.14 | 0.43 |
| | B42E | 0 | 0 | 42 | 9 | High | Refuge | 0 | 0 | Refuge | 0 | 0.03 |
| | B71C | 0 | 0 | 263 | 8 | High | Refuge | 0 | 0.2 | Refuge | 0 | 0.24 |
| | B71G | 0 | 0 | 246 | 40 | High | Refuge | 0 | 0.3 | Refuge | 0 | 0.25 |
| | B72F | 0 | 0 | 81 | 8 | High | Refuge | 0 | 0.1 | Refuge | 0 | 0.1 |
| | A42H | 12 | 14 | 1 057 | 8 | High | Ecological Trap | 9.86 | -1.8 | Ecological Trap | 18.32 | -4.18 |
| | A50D | 3 | 7 | 638 | 2 | High | Ecological Trap | 7.38 | -0.7 | Ecological Trap | 10.54 | -1.32 |
| | A50C | 0 | 3 | 362 | 2 | High | Ecological Trap | 4.88 | -0.2 | Ecological Trap | 4.88 | -0.16 |
| | A42G | 19 | 13 | 1 206 | 6 | High | Ecological Trap | 7.01 | -1.3 | Ecological Trap | 17.25 | -5.06 |
| | A50F | 5 | 5 | 372 | 2 | High | Ecological Trap | 10.02 | -0.6 | Ecological Trap | 20.05 | -1.64 |
| | A42F | 14 | 6 | 1 022 | 1 | High | Ecological Trap | 4.12 | -0.2 | Ecological Trap | 13.74 | -2.95 |
| | B73D | 0 | 0 | 14 | 6 | Very High | Refuge | 0 | 0 | Refuge | 0 | 0.01 |
| | A23B | 0 | 0 | 6 | 8 | Very High | Refuge | 0 | 0 | Refuge | 0 | 0 |
| | A23L | 0 | 0 | 2 | 7 | Very High | Refuge | 0 | 0 | Refuge | 0 | 0 |
| | A24A | 0 | 0 | 14 | 7 | Very High | Refuge | 0 | 0 | Refuge | 0 | 0 |
| | B32A | 0 | 0 | 1 | 8 | Very High | Refuge | 0 | 0 | Refuge | 0 | 0 |
| | A23F | 0 | 0 | 3 | 8 | Very High | Refuge | 0 | 0 | Refuge | 0 | 0 |
| | A32B | 0 | 0 | 0 | 1 | Very High | NA | NA | NA | NA | NA | NA |
| Municipality | Greater Giyani | 1 | 1 | 2994 | 79 | Low | Refuge | 0.9 | 0.6 | Refuge | 1.8 | 0.4 |
| | Greater Letaba | 3 | 0 | 1896 | 112 | Low | Refuge | 0 | 0.83 | Refuge | 2.61 | 0.23 |
| | Thulamela | 0 | 0 | 2910 | 197 | Low | Refuge | 0 | 1.15 | Refuge | 0 | 1.15 |
| | Aganang | 0 | 1 | 1883 | 71 | Low | Refuge | 1.57 | 0.26 | Refuge | 1.57 | 0.26 |
| | Molemole | 1 | 4 | 3353 | 33 | Low | Refuge | 2.23 | 0.49 | Refuge | 2.79 | 0.29 |
| | Polokwane | 1 | 0 | 3772 | 165 | Low | Refuge | 0 | 1.17 | Refuge | 0.61 | 0.97 |
| | Ephraim Mogale | 2 | 0 | 2014 | 67 | Low | Refuge | 0 | 0.79 | Refuge | 1.82 | 0.39 |
| | Makhuduthamaga | 1 | 0 | 2101 | 132 | Low | Refuge | 0 | 0.53 | Refuge | 1.36 | 0.33 |
| | Fetakgomo | 0 | 0 | 1107 | 85 | Low | Refuge | 0 | 0.48 | Refuge | 0 | 0.48 |
| | Mutale | 0 | 0 | 2640 | 46 | Medium | Refuge | 0 | 1.28 | Refuge | 0 | 1.28 |
| | Lepele Nkumpi | 2 | 1 | 3470 | 69 | Medium | Refuge | 0.34 | 1.94 | Refuge | 1.01 | 1.54 |
| | Elias Motsoaledi | 2 | 1 | 3716 | 67 | Medium | Refuge | 0.41 | 1.57 | Refuge | 1.22 | 1.17 |
| | Greater Tubatse | 8 | 1 | 4613 | 70 | Medium | Refuge | 0.22 | 3.06 | Refuge | 1.99 | 1.46 |
| | Greater Tzaneen | 6 | 5 | 3252 | 120 | Medium | Refuge | 2.05 | 0.76 | Ecological Trap | 4.51 | -0.44 |
| | Thabazimbi | 72 | 28 | 11176 | 8 | Medium | Refuge | 3.16 | 0.78 | Ecological Trap | 11.28 | -13.62 |
| | Mookgopong | 16 | 11 | 5694 | 7 | Medium | Refuge | 2.62 | 0.83 | Ecological Trap | 6.42 | -2.37 |
| | Modimolle | 15 | 16 | 4680 | 15 | Medium | Refuge | 3.08 | 0.54 | Ecological Trap | 5.96 | -2.46 |
| | Bela Bela | 14 | 4 | 3405 | 20 | Medium | Refuge | 1.84 | 0.77 | Ecological Trap | 8.26 | -2.03 |
| | Mogalakwena | 25 | 10 | 6171 | 46 | Medium | Refuge | 1.84 | 1.91 | Ecological Trap | 6.44 | -3.09 |
| | Phalaborwa | 17 | 12 | 3019 | 47 | Medium | Ecological Trap | 3.71 | -0.07 | Ecological Trap | 8.97 | -3.47 |
| | Maruleng | 7 | 23 | 3256 | 29 | Medium | Ecological Trap | 6.84 | -2.18 | Ecological Trap | 8.92 | -3.58 |
| | Musina | 19 | 69 | 7585 | 7 | Medium | Ecological Trap | 10.92 | -9.25 | Ecological Trap | 13.93 | -13.05 |
| | Makhado | 32 | 36 | 8317 | 62 | Medium | Ecological Trap | 4.47 | -1.4 | Ecological Trap | 8.44 | -7.8 |
| | Blouberg | 45 | 36 | 9253 | 18 | Medium | Ecological Trap | 4.74 | -1.73 | Ecological Trap | 10.66 | -10.73 |
| | Lephalale | 114 | 95 | 13780 | 8 | Medium | Ecological Trap | 6.56 | -8.57 | Ecological Trap | 14.42 | -31.37 |
| District | Sekhukhune | 13 | 2 | 13551 | 80 | Medium | Refuge | 0.21 | 6.43 | Refuge | 1.58 | 3.83 |
| | Capricorn | 49 | 42 | 21731 | 58 | Medium | Refuge | 2.87 | 2.13 | Ecological Trap | 6.22 | -7.67 |
| | Mopani | 34 | 41 | 14417 | 75 | Medium | Ecological Trap | 3.63 | -0.07 | Ecological Trap | 6.64 | -6.87 |
| | Vhembe | 51 | 105 | 21451 | 59 | Medium | Ecological Trap | 5.92 | -8.23 | Ecological Trap | 8.8 | -18.43 |
| | Waterberg | 256 | 164 | 44905 | 15 | Medium | Ecological Trap | 4.06 | -3.73 | Ecological Trap | 10.4 | -54.93 |

A number of mortality events attributed to that particular source of offtake

B human census data were obtained from Statistics South Africa (2011) and defined as the number of people per $km^2$

C the difference required in the number of leopards killed per annum to meet the 3.6% sustainability threshold

## 2.8 TABLES AND FIGURES

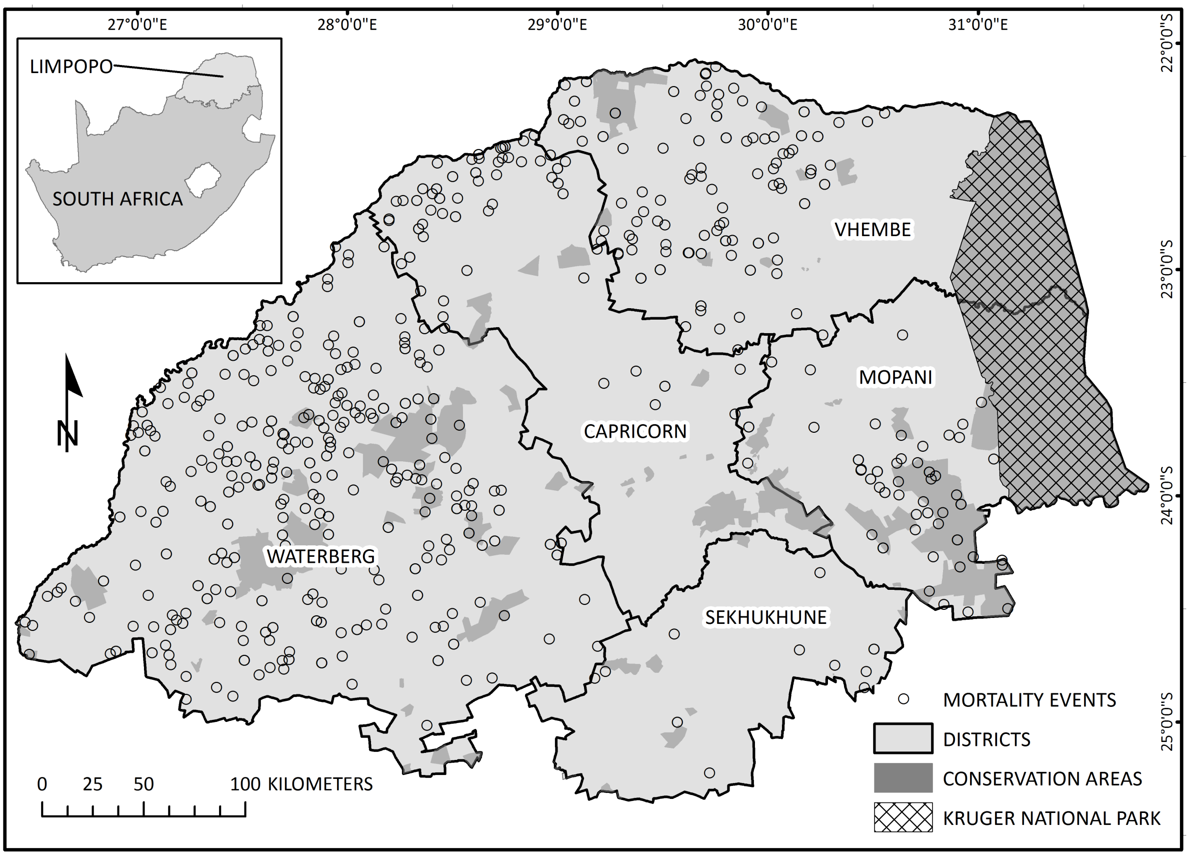

Figure 2.1. Distribution of leopard *(Panthera pardus)* mortality events (*N* = 757) from January 2007 to December 2012 across Limpopo Province, South Africa. The Kruger National Park (cross-hatched) was removed from all analyses; dark-grey areas represent the remaining conservation areas.

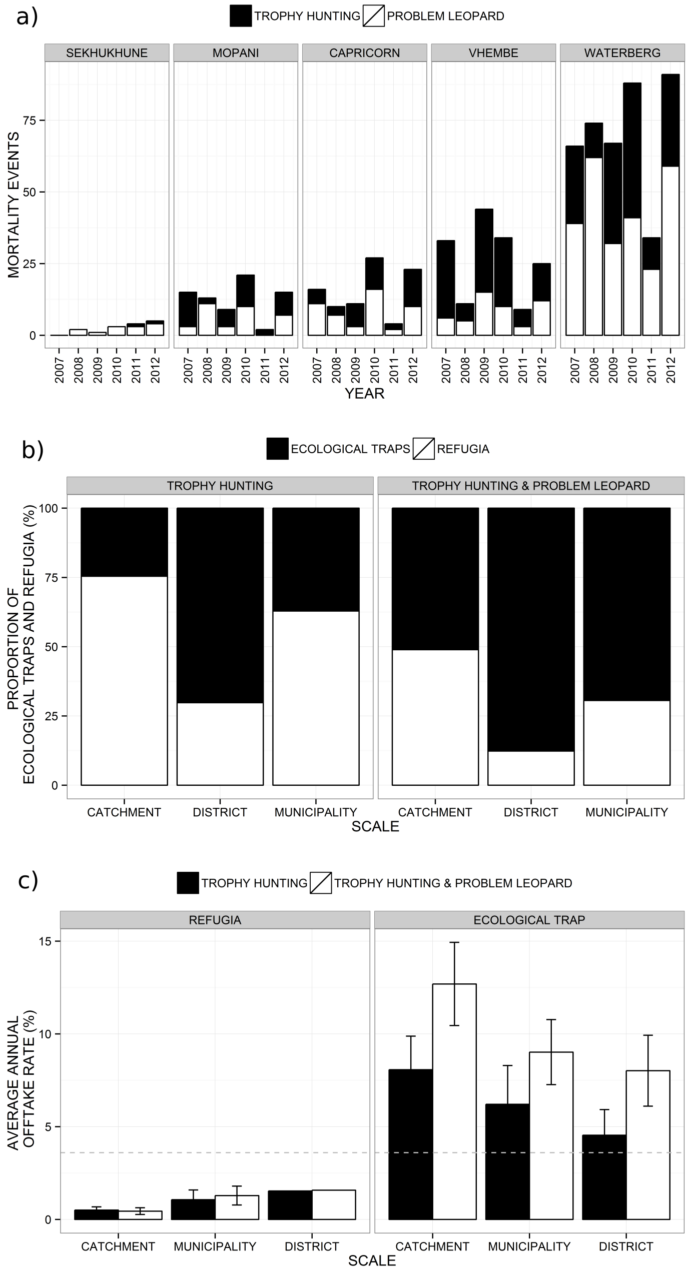

Figure 2.2. Leopard *(Panthera pardus)* mortality events from trophy hunting and problem leopard permits distributed temporally across the five current management districts of Limpopo Province, South Africa from 2007–2012 (a); proportion of *de facto* refugia and ecological traps at three geographical scales under two offtake scenarios for Limpopo Province, South Africa from 2007–2012 (b); and average annual leopard offtake rates (95% CI) at three geographical scales (dashed line depicts the 3.6% sustainable offtake rate) under two offtake scenarios for Limpopo Province, South Africa from 2007–2012 (c).

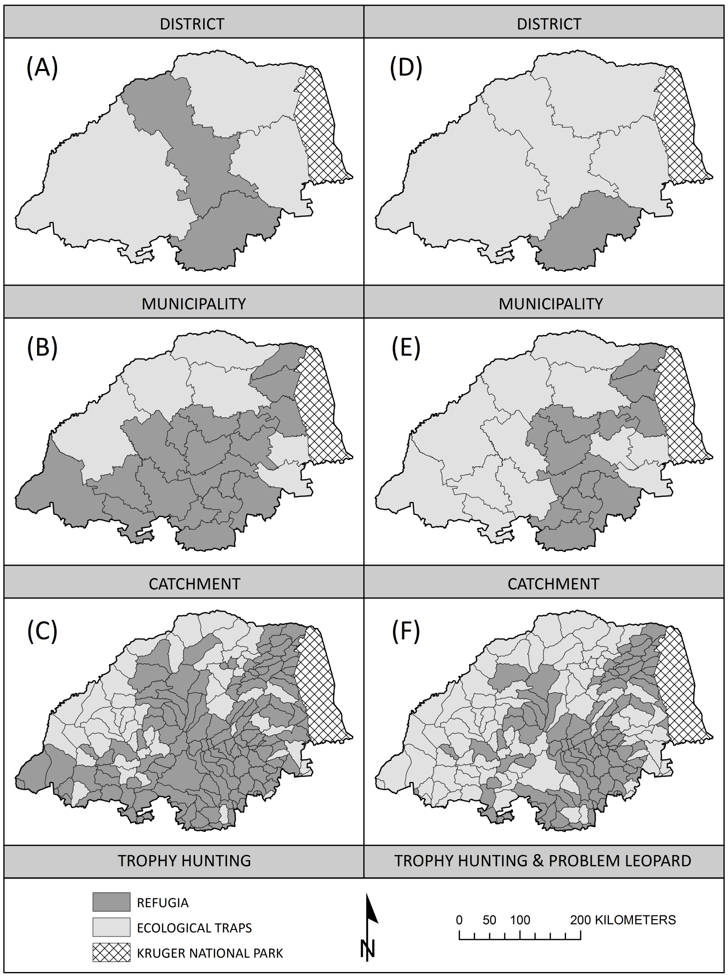

Figure 2.3. Distribution of *de facto* refugia and ecological traps under two offtake scenarios (trophy hunting A–C and trophy hunting and problem leopard D–F) at the catchment- (C and F), municipal- (B and E), and district-scale (A and D) across Limpopo Province, South Africa.

# CHAPTER 3 – The conservation costs of game ranching

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## 3.1 ABSTRACT

The devolution of user rights of wildlife in southern Africa has led to a widespread land-use shift from livestock farming to game ranching. The economic advantages of game ranching over livestock farming are significant, but so too are the risks associated with breeding financially valuable game where free-ranging wildlife pose a credible threat. Here, we assessed whether the conservation potential of game ranching, and a decentralized approach to conservation more generally, may be undermined by an increase in human-wildlife conflict. We demonstrate that game rancher tolerance towards free-ranging wildlife has significantly decreased as the game ranching industry has evolved. Our findings reveal a conflict of interest between wealth and wildlife conservation resulting from local decision-making in the absence of adequate centralized governance and evidence-based best practice. As a fundamental pillar of devolution-based natural resource management, game ranching proves an important mechanism for economic growth, albeit at a significant cost to conservation.

## 3.2 INTRODUCTION

The governance of natural resources has historically resided with the state (Child 2004). However, decentralization of governance has produced a devolutionary shift in natural resource management over the past four decades (Parker, Thapa & Jacob 2015), particularly in developing countries (Ribot, Agrawal & Larson 2006; Larson & Soto 2008). This shift to local resource management is based on the premise that local people are committed to sustainable resource use (Cousins, Sadler & Evans 2008). In southern Africa, policies that once established centralized control over wildlife were replaced by legislative changes that bestowed custodial rights of wildlife to individual property owners (Bothma, Suich & Spenceley 2009; Lindsey, Romanach & Davies-Mostert 2009b). Following the mantra “if it pays, it stays”, southern African governments sought to align environmental management objectives with the socio-economic needs of local people (Child 2004). This devolution-based legislation encouraged innovation among the private and communal sectors (Child 2012a), resulting in a rapid and widespread land-use shift in rangelands from livestock farming to game ranching (Cloete, Taljaard & Grove 2007; Lindsey, Romanach & Davies-Mostert 2009a).

Game ranching in southern Africa is now synonymous with private- and community-based natural resource management (Bothma, Suich & Spenceley 2009). Although largely perceived to benefit environmental conservation through the protection of habitat and biodiversity (Lindsey, Romanach & Davies-Mostert 2009a), game ranching inherently increases interactions—and potentially conflict—between valuable game species and free-ranging wildlife (Lindsey *et al.* 2013c). Many free-ranging large mammals across southern Africa are ecologically vital as keystone species, and act as biodiversity indicators (Dalerum *et al.* 2008), but typically accrue little direct financial benefit to game ranchers. In contrast, commercial game species represent important agricultural assets that represent substantial financial resources (Van Der Merwe, Saayman & Krugell 2004). Ranchers are therefore unlikely to tolerate (defined here as the willingness to accept an event despite challenging circumstances; adapted from (Treves & Naughton-Treves 2005) free-ranging wildlife potentially threatening those assets through depredation or infrastructure damage. Decreased tolerance may be further intensified by economic instability (Dickman 2010), particularly as agricultural sectors can act as economic buffers during periods of financial crises (Headey, Malaiyandi & Fan 2010), which often result in increased investment and financial reliance on agricultural productivity (Headey, Malaiyandi & Fan 2010; Allen & Giovannetti 2010).

Limpopo Province, South Africa (ca. 125 977 km$^2$; hereafter ‘Limpopo’, Fig. 3.1), has a largely impoverished human population, the highest density of game ranches in South Africa (Carruthers 2008), and an abundance of free-ranging wildlife. Game ranch establishment peaked across South Africa, and particularly in Limpopo (van der Waal & Dekker 2000), during the early 1990s (Van Der Merwe, Saayman & Krugell 2004), with expansion subsequently reducing by the turn of the millennium (van der Waal & Dekker 2000;

Bothma & Sartorius Von Bach 2010). Game ranching represents a core component of the agricultural sector, and has recently shifted from breeding large numbers of common game species towards breeding fewer high-value species with increasingly intensive management (Lindsey, Romanach & Davies-Mostert 2009a) (Supporting Information S3.1). This land-use shift may exacerbate levels of conflict by increasing the financial threat posed by free-ranging wildlife and possibly result in increased adoption of conflict mitigation measures, such as problem animal control, or the use of heavily fortified predator-proof fencing (Lindsey et al. 2011). Here, we assess whether the conservation potential of game ranching, and a decentralized approach to conservation more generally, may be undermined by an increase in human-wildlife conflict in Limpopo from 2003–2012. We explore the evolution of game ranching practices from extensive to intensive, to better understand the concomitant change in game rancher tolerance of free-ranging wildlife, and integrate this mechanistic understanding into the challenges facing conservation policy making more generally.

We hypothesized that given the economic reliance on agriculture during times of financial crises, investment within the agricultural sector (e.g., game ranching) should have increased around the global economic crisis of 2008, which severely impacted South Africa (Allen & Giovannetti 2010). We expected that as game ranching profitability increases, tolerance towards free-ranging wildlife that threaten game ranching assets should decrease. Finally, we predicted that decreased tolerance should lead to increased problem animal control, and increased predator-proof fencing, in an attempt to reduce interactions between valuable game and free-ranging wildlife that pose a significant threat.

## 3.3 METHODOLOGY

### 3.3.1 Measuring the scale and profitability of game ranching

Limpopo's annual game auction records, comprising numbers of game sold, average price, and annual turnover (i.e., annual sales volume) for each species, were obtained from the Vleissentraal online database (www.vleissentraal.co.za; accessed December 2013). Livestock auction records of economically important breeds (e.g., Bonsmara cattle *Bos taurus*, Merino and Dorper sheep *Ovis aries*) were obtained from Farmer's Weekly archives (National Library of South Africa, Pretoria). Game were categorized into common breeds and high-value breeds based on their maximum average price (common game ≤ ZAR 10 000; high-value game > ZAR

10 000 per animal) over the study period. Return of investment (i.e., amount of financial return relative to investment cost) of game and livestock was quantified by pooling males and females of adults only, using their value at auction. National and provincial economic data were obtained from Statistics South Africa (www.statssa.gov.za; statistical release P0441, accessed December 2013) from 2003–2012. Auction and economic data were standardized using the buying power (1 + (Consumer Price Index / 100) * yearly value) of the South African Rand (CPI source: www.inflation.eu).

### 3.3.2 Identifying land-use types

Using a geographic information system (GIS), we divided Limpopo into different land-use types by overlaying formally registered game ranches (Exemption Property Database, LEDET), protected areas (World Database on Protected Areas; IUCN and UNEP-WCMC, accessed December 2014), natural and man-made water bodies (Department of Agriculture, Forestry and Fisheries), urban and rural settlements (Statistics South Africa), and agricultural land (Department of Agriculture, Forestry and Fisheries), with the remainder comprising mixed farms. Mixed farms in Limpopo predominantly practice game ranching, interspersed with livestock farming. Game ranches may act as small pseudo-protected areas by restoring habitat and introducing species, but are fundamentally different to protected areas in how they are managed (Bond *et al.* 2004). Game ranch management is profit-orientated with emphasis on the commercial production of ungulate species (Bothma & Sartorius Von Bach 2010), whereas protected area management is largely conservation-orientated (Leverington *et al.* 2010). Therefore, to avoid potential bias relating to the management of protected areas (e.g., problem animal control on protected areas is likely driven by underlying conservation objectives such as disease control, rather than financial motivations), we excluded protected areas from our analyses. Land-use types were then categorized into ‘non-game ranches’ comprising agricultural land and urban and rural settlements, and ‘game ranches’ comprising formally registered game ranches and mixed farms.

### 3.3.3 Measuring conflict as a proxy for landowner tolerance

In Limpopo, problem animal permits are issued to landowners by the Limpopo Department of Economic Development, Environment and Tourism (LEDET), for the destruction of animals that reputedly pose a risk to human life or livelihoods. To measure conflict, we used the number of problem animal permit applications issued from 2003–2012 (Wildlife Trade and Regulation Archives, LEDET). Problem animal permit applications, whether approved or rejected, represent the intent of a landowner to destroy a putative problem animal, and therefore provides a reliable gauge of tolerance. We acknowledge that human attitudes towards nuisance wildlife are multi-dimensional (Kansky, Kidd & Knight 2014), yet justify our approach on the basis that tolerance levels likely degrade to a point where landowners perceive legal destruction as a potential solution. Free-ranging wildlife that potentially threaten the profitability of the game ranching industry include black-back jackal *Canis mesomelas*, brown hyaena *Hyaena brunnea*, caracal *Caracal caracal*, cheetah *Acinonyx jubatus*, lion *Panthera leo*, leopard *Panthera pardus*, spotted hyaena *Crocuta crocuta*, and African elephant *Loxodonta africana* (collectively referred to as 'nuisance wildlife'). We also collected problem animal permit applications for greater kudu *Tragelaphus strepsiceros* and common duiker *Sylvicapra grimmia* ('non-nuisance wildlife'), as these two common ungulate species are frequently complicit in human-wildlife conflict, but represent a minimal threat to game ranching profitability. Global positioning system (GPS) coordinates for the property location of each problem animal permit application were obtained from the Chief Surveyor General's registered property database (Cadastral Spatial Information, Pretoria). Permit locations were projected across Limpopo, and assigned a land-use category based on the underlying property.

### 3.3.4 Identifying game ranching practices

An online survey was conducted to assess how Limpopo's game ranching practices have changed over the study period (respondent sample size = 116; Supporting Information S3.2). Given the increasing prices of game across southern Africa (Van Der Merwe, Saayman & Krugell 2004), ranchers were asked whether they (1) breed rare game (e.g., roan antelope *Hippotragus equinus*, sable antelope *Hippotragus niger*, buffalo *Syncerus caffer*), (2) breed colour variants (e.g., black impala *Aepyceros melampus*, copper springbok *Antidorcas marsupialis*), and (3) breed extralimital game (i.e., species that do not occur naturally in their region). Only rare game and colour variants were considered 'high-value' species. Finally, given the increasing scientific debate around fencing for wildlife (Woodroffe, Hedges &

Durant 2014), ranchers were asked whether they used predator-proof fencing. All questions required the year in which the particular practice was first adopted.

### 3.3.5 Statistical Analysis

Generalized linear models were used to assess trends over time in game auction sales, game ranching practices, and problem animal permit applications. All statistical analyses were conducted within R v.3.2.0 (R Core Team 2016). All data used in the analyses are available in Supporting Information S3.3.

## 3.4 RESULTS

### 3.4.1 Economic contribution of game ranching

Limpopo's agricultural industry generated ZAR 27.64 billion (US$ 1.96 billion) from 2003–2012. The global economic crisis of 2008 lead to an economic recession in South Africa (Supporting Information S3.4), which resulted in negative growth for all industries other than agriculture (Supporting Information S3.5). Game ranching contributed 2.8 ± 0.3% (SE) to the growth in Limpopo's agricultural gross domestic product (GDP) prior to the recession (2003–2007), and 12.8 ± 4.6% (SE) during and after the recession (2008–2012). High-value game breeding was a far greater contributor to GDP than common game breeding over the 10-year period (Fig. 3.2b). Investing in high-value game breeding in 2008 would have resulted in a return on investment (ROI) of 187% by the end of 2012, whereas breeding common game would have returned 57% over the same period. Compared to high-value game, breeding of South Africa's common livestock species, such a Bonsmara cattle (ROI: 60%), or Merino (ROI: 103%) and Dorper sheep (ROI: 7%), would have resulted in far smaller returns on investment.

### 3.4.2 Game ranching practices and trends in Limpopo

The average price (Table 3.1a; Fig. 3.3b) and annual turnover (Table 3.1b; Fig. 3.3c) of game sold in Limpopo increased significantly over the 10-year study period. This primarily reflected a significant increase in the number (Table 3.1c; Fig. 3.3a) and price (Table 3.1d; Fig. 3.3b) of high-value species sold by game ranchers, particularly after 2008. In contrast, the number of common species sold decreased significantly over the 10-year period (Table 3.1e; Fig. 3.3a).

Game ranchers consistently paid higher prices for female high-value game, than for males (Fig. 3.2a), highlighting the importance of breeding rather than hunting. As the number of game ranchers breeding high-value species significantly increased over the 10-year period (Table 3.1f; Fig. 3.4a; n = 104), so did the number of ranchers using predator-proof fencing (Table 3.1g; Fig. 3.4b; n = 94).

### 3.4.3 Measuring conflict and understanding game rancher tolerance

From 2003–2012, landowners submitted 693 problem animal permit applications for nuisance wildlife, and 999 for non-nuisance wildlife. Most (79%) applications originated from game ranches. For nuisance wildlife, leopard were the most common putative problem animal (68%), followed by elephant (20%), lion (4%), brown hyaena (3%), black-backed jackal (2%), caracal (2%), cheetah (0.5%), and spotted hyaena (0.5%). Applications by game ranchers for nuisance wildlife increased significantly (Table 3.1h; Supporting Information S3.6a) over the 10-year period, whereas no significant relationship was detected for nuisance wildlife on non-game ranches (Table 3.1i; Supporting Information S3.6b). Applications for non-nuisance wildlife on game ranches however approached significance (Table 3.1j; Supporting Information S3.6c), indicating an underlying positive trend. The number of applications for nuisance wildlife increased significantly with the number of game ranchers breeding high-value species (Table 3.1k; Fig. 3.5a), and with the use of predator-proof fencing (Table 3.1l; Fig. 3.5b). Problem animal permit applications for elephant, which damage fences (Mutinda *et al.* 2014), began only once the use of predator-proof fencing had markedly risen from 2008 (Fig. 3.4b).

## 3.5 DISCUSSION

The global shift from centrally driven decision-making to a decentralized, local participatory process is argued to represent a more legitimate and inclusive governance system that improves local livelihoods and conservation outcomes (Parker, Thapa & Jacob 2015). Game ranching is widely heralded as a conservation success and epitomizes the devolutionary rights-based approach to natural resource management in southern Africa (Carruthers 2008; Cousins, Sadler & Evans 2008). Yet, here we highlight the hidden costs of local decision-making in the absence of adequate centralized regulation and evidence-based best practice necessary to uphold conservation objectives. We demonstrate that game ranching has become an important and highly lucrative sector within the agricultural industry. Game ranching practices have become more intensive, to facilitate the breeding of high-value game species. In response to the increased profitability of game breeding, ranchers have adopted a dual-pronged approach to asset management by increasing predator-proof fencing to keep free-ranging wildlife out, and reducing populations of nuisance wildlife through legal destruction. Our findings demonstrate that the proportional increase in problem animal control of nuisance wildlife has far outweighed the proportional increase in game ranching trends towards more intensive practices—suggesting that intolerance is growing in momentum. The consequences of decreased tolerance towards ecologically important free-ranging wildlife is likely to have significant detrimental impacts on species persistence and ecological systems more broadly (Ripple *et al.* 2014; 2015).

Unreported and illegal killing of wildlife is a pertinent issue across southern Africa (St John *et al.* 2012; Thorn *et al.* 2013; Kahler & Gore 2015). Human-mediated carnivore mortality is widespread, especially amongst livestock and game ranchers in Limpopo (St John *et al.* 2012). A recent study on leopards in Limpopo demonstrated that legal mortality is unsustainable (Pitman *et al.* 2015), and camera-trapping surveys conducted during and after the study period indicate that leopard populations are declining (Supporting Information S3.7). Elephant populations in the region are increasing at 4% per annum (Blanc 2008), but this growth is primarily confined to protected areas (a land-use type removed from this study). Interestingly, permit applications for elephants only began from 2008—the same year in which predator proof fencing markedly increased. This may suggest that predator proof fencing has not only failed to mitigate some forms of conflict in Limpopo, but actively contributed to decreased tolerance towards elephants. Game ranch expansion into new territories decelerated by the late 1990's (van der Waal & Dekker 2000; Bothma & Sartorius Von Bach 2010), which suggests that game ranching territory has not increased over the study period. Notably, Limpopo's human population has markedly grown (8.2% increase from 2001 to 2011; Statistics South Africa 2011), which has left the majority of suitable wildlife habitat in a highly fragmented state (Swanepoel *et al.* 2013).

Given the high returns on investment, the shift towards high-value game breeding has been, and continues to be, rapidly adopted across the region. From an economic standpoint, game ranching is a significant contributor and is likely to remain an important component on political and economic agendas. Agricultural sectors are considered informal economic safety nets during periods of financial crises (Headey, Malaiyandi & Fan 2010). This is particularly relevant for developing countries where agricultural products are not highly exported, and the inherent inelasticity of the agricultural sector to economic downturn (Shovan 2004; Headey, Malaiyandi & Fan 2010). Given the increased economic reliance on agricultural productivity, and the increased financial risk associated with intensive high-value game breeding, decreased tolerance among landowners towards putative problem animals appears inevitable. The adoption of integrated conservation and development projects (ICDPs), and local resource management more generally, is often put forward as a viable conflict mitigation option (Treves, Wallace & White 2009). However, the effectiveness of ICDPs have been mixed, particularly in regard to human-wildlife conflict (Gandiwa *et al.* 2013). Attitudes around human-wildlife coexistence are primarily influenced by how conflict is managed, and importantly, the severity of conflict events (Don Carlos *et al.* 2009). As the value of commercial game increases, and consequently the severity of conflict, attitudes towards nuisance wildlife become increasingly antagonistic. The propensity to erect predator-proof fencing in response to conflict raises further concerns (Woodroffe, Hedges & Durant 2014), as it can fragment habitat and significantly alter interactions between species, leading to detrimental impacts on ecosystem functions (Terborgh *et al.* 2001; Ripple *et al.* 2014).

The top three species killed as putative problem animals (leopards, elephants and lions) are also the most desired for non-consumptive tourism (Di Minin *et al.* 2013). The contribution of charismatic species to a country’s economy, together with their ecological significance, make them vitally important species to conserve (Richardson & Loomis 2009). Game ranching has become established in other southern African countries; including Botswana, Namibia, Zambia and Zimbabwe (Bond *et al.* 2004; Lindsey, Romanach & Davies-Mostert 2009a). In addition, we highlight an issue limited not only to Africa, as European countries (e.g., Spain) have also demonstrated decreased tolerance towards large carnivores following the adoption of intensive game management practices (López-Bao *et al.* 2015). Threatened species within these countries require extensive rangelands to maintain large and biologically viable populations (Graham *et al.* 2009). The adoption of game ranching is largely perceived to be a compatible land-use option for the protection of these threatened species (Cousins, Sadler & Evans 2008). However, the increased use of predator-proof fencing and legal destruction of wildlife in Limpopo, suggests that game ranching practices have become less compatible with species conservation.

Given the scale of decentralization and the widespread adoption of game ranching, together with the economic instability faced by countries within southern Africa, further research is required to quantify the extent to which ecologically important species are persecuted as a result of intensive game ranching practices. In South Africa, game ranching trends are currently accelerating, with high-value species being sold at record prices (e.g., sable antelope bull and kudu bull sold for ZAR 27 million (US$ 1.9 million) and ZAR 9.4 million (US$ 0.7 million) in 2015, respectively; www.vleissentraal.co.za; date accessed: 29 September 2015). By bestowing custodial rights of wildlife to individual property owners, legislative policies encouraged innovation among the private and communal sectors that has ultimately inflicted a significant cost to wildlife conservation. Given these findings, devolution-based natural resource management likely requires increased centralized regulation to limit, or better control, the widespread adoption of intensive game ranching practices and their negative consequences on large scale conservation objectives. Increased centralized regulation likely provides a more scientifically-justified, holistic approach to land management and conservation, but may also present significant disadvantages. Limiting the use of wildlife may diminish their value and make them an intolerable financial burden (Murombedzi 2003), whilst centralized governance may disempower individuals and communities (Carruthers 2008), leading to non-compliance in conservation objectives and a general distrust towards governing authorities. The solution to the conservation issue we highlight therefore requires adept consideration of all stakeholders within a transparent and science-based framework.

## 3.6 ACKNOWLEDGEMENTS

This research was funded by Panthera. We are grateful to Wildlife Ranching South Africa and the South African Hunters and Game Conservation Association for distributing the online survey, and to Lourens Swanepoel and Julia Chase Grey for providing historical camera-trapping data. Ethical clearance for the online survey was approved by the University of KwaZulu-Natal's ethics committee (protocol reference number: HSS/0938/013M). RTP was supported by a South African National Research Foundation bursary (# 83690) and a Panthera

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## 3.7 SUPPORTING INFORMATION

Supporting Information S3.1. Game breeding fashions. Game ranchers across Limpopo Province, South Africa breed (a) high-value game breeds such as sable antelope *Hippotragus niger*, and (b) common game breeds such as greater kudu *Tragelaphus strepsiceros*. Naturally rare game (e.g., sable antelope) are regarded as 'glamour' breeds, which fetch high prices at auction and as hunting trophies. Across southern Africa there has been a surge in the breeding of aberrant colour variants (Lindsey, Romanach & Davies-Mostert 2009a) (also known as 'designer' breeds), which are selected through intensive breeding of related individuals with the purpose of expressing recessive morphological traits (e.g., black impala *Aepyceros melampus*). Designer breeds fetch exorbitantly high prices at auction, but are seldom hunted due to their high price. *Images courtesy of Charles James Sharp.*

Supporting Information S3.2. Details of game ranch survey.

An electronic survey was distributed in English and Afrikaans by Wildlife Ranching South Africa (WRSA) and the South African Hunters and Game Conservation Association (SAHGCA) from 1st August 2014 – 14th November 2014. Response rate from SAHGCA members was poor, such that all data originating from SAHGCA were removed from all analyses. Although the number of game ranches across Limpopo is unknown, the majority of game ranch owners are likely to be WRSA members. We therefore assume our available sample group provides a comprehensive representation of game ranch practices across Limpopo. The survey comprised two sections, which took approximately three minutes to complete. All registered WRSA members were emailed a request to participate. The survey was completed by game ranch owners only. The sample group consisted of approximately 840 members. However, the sample group size is an overestimate of the total number of qualifying respondents (i.e., game ranch owners), since family members of game ranch owners are also registered WRSA members. Only rare game and colour variants were considered 'high-value' species. A total of 116 respondents participated in the survey. Twelve respondents were disqualified from all 'predator proof fencing' analyses for failing to provide the year in which they adopted the practice. One participant, from the initial twelve, was disqualified from all analyses for failing to provide all temporal information. If any practices were adopted before 2003, they were totaled and added to the annual value for 2003; therefore 2003 acted as a baseline starting point for analysis. If respondents provided either 2013 or 2014 as years when a particular practice was adopted, their data were omitted from all analyses since these data fell outside of our study period. Analyses concerning the adoption of high-value game breeding comprised 104 respondents, whilst analyses concerning the adoption of predator proof fencing comprised 94 respondents.

Visual examples of the survey, comprising section 1 and section 2:

## Section 1

*** 1. Please select in which Limpopo district your game farm is located:**
**Dui asseblief aan in watter distrik in Limpopo u wildsplaas geleë is:**

○ Waterberg

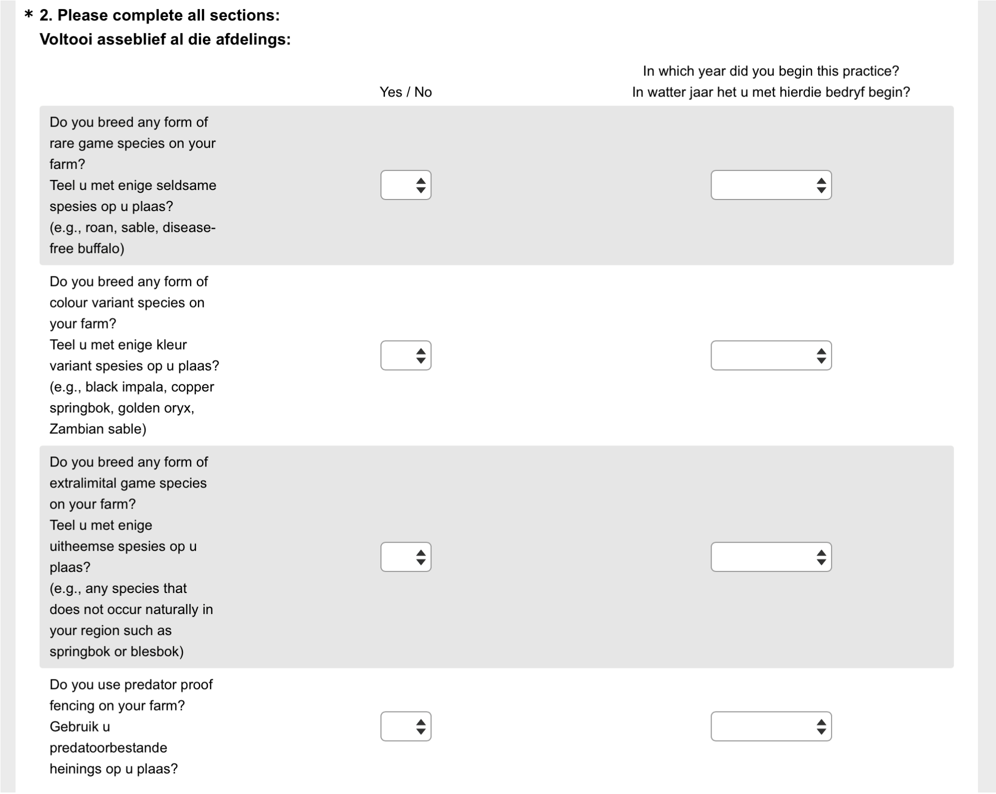
○ Capricorn

○ Vhembe

○ Mopani

○ Sekhukhune

## Section 2



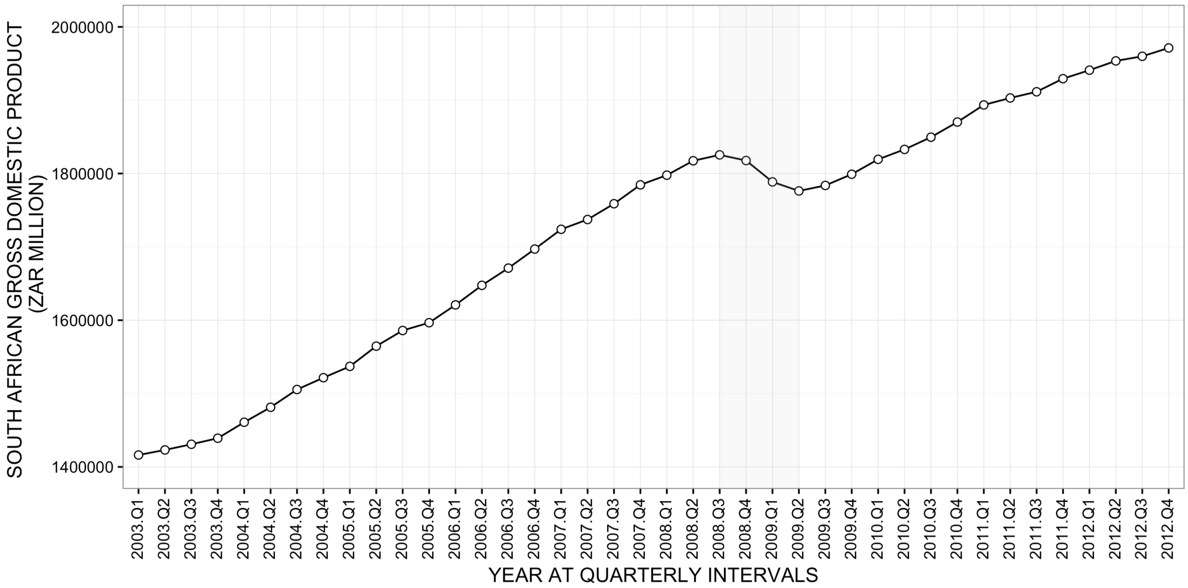
*** 2. Please complete all sections:**
**Voltooi asseblief al die afdelings:**

| | Yes / No | In which year did you begin this practice?<br>In watter jaar het u met hierdie bedryf begin? |
|---|---|---|
| Do you breed any form of rare game species on your farm?<br>Teel u met enige seldsame spesies op u plaas?<br>(e.g., roan, sable, disease-free buffalo) | | |
| Do you breed any form of colour variant species on your farm?<br>Teel u met enige kleur variant spesies op u plaas?<br>(e.g., black impala, copper springbok, golden oryx, Zambian sable) | | |
| Do you breed any form of extralimital game species on your farm?<br>Teel u met enige uitheemse spesies op u plaas?<br>(e.g., any species that does not occur naturally in your region such as springbok or blesbok) | | |
| Do you use predator proof fencing on your farm?<br>Gebruik u predatoorbestande heinings op u plaas? | | |

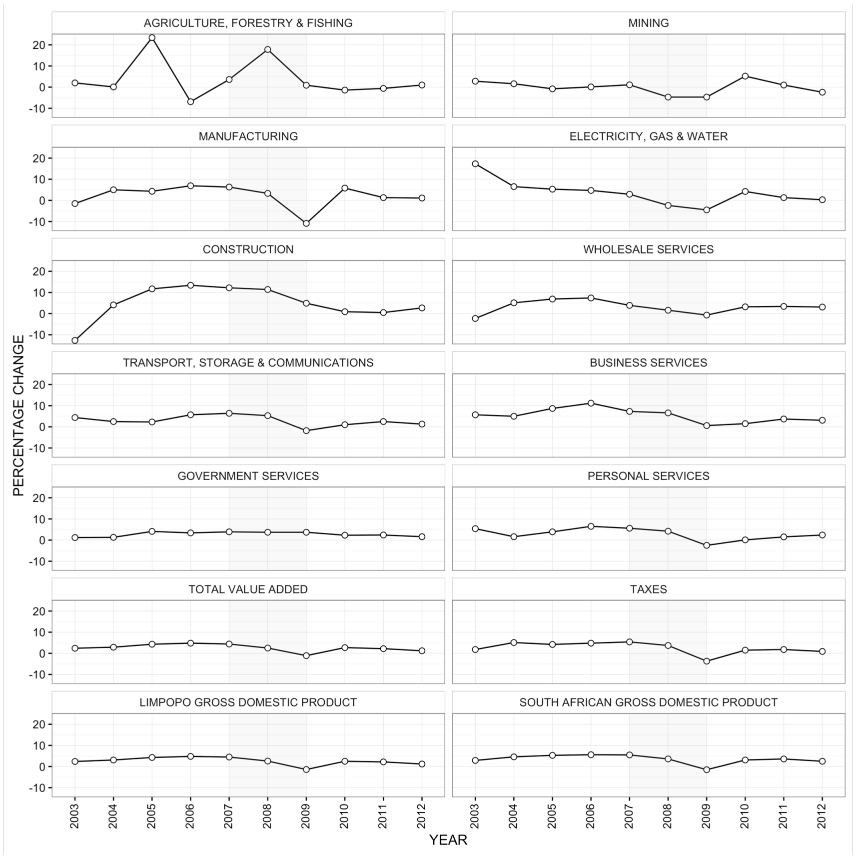
Supporting Information S3.3. Datasets

Data are available at the publisher’s website.

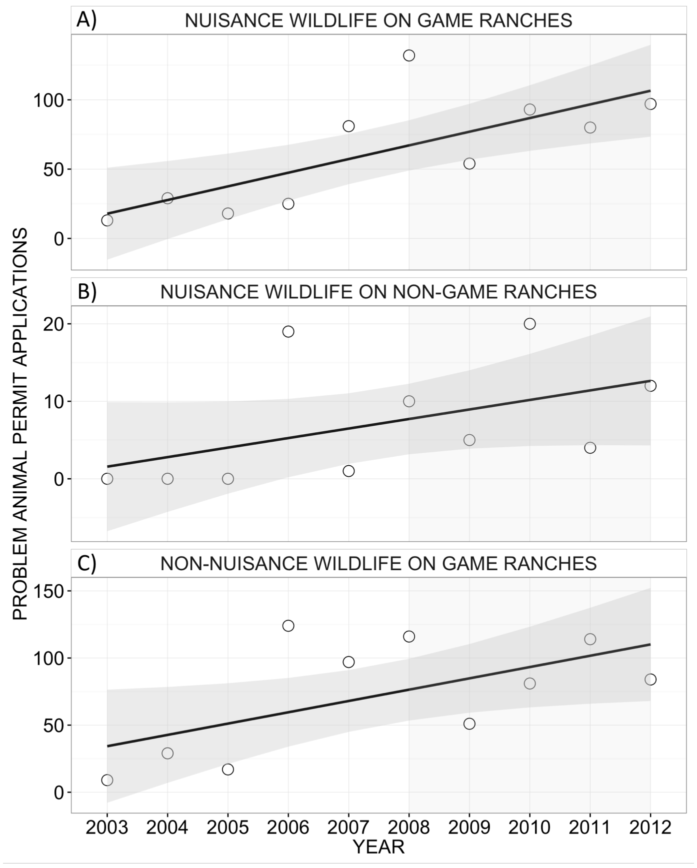
Supporting Information S3.4. South African gross domestic product (GDP). Using quarterly intervals from 2003–2012 (ZAR; Vertical grey bar represents the onset of the economic recession). Data sourced from Statistics South Africa.



Supporting Information S3.5. Percentage change in gross domestic product (GDP). Gross domestic product by industry for South Africa from 2003–2012 (Vertical grey bar represents the onset of the economic recession). Data sourced from Statistics South Africa.



Supporting Information S3.6. Legal destruction of free-ranging wildlife. Problem animal permit applications for (a) nuisance wildlife on game ranches (statistically significant, positive trend identified), (b) nuisance wildlife on non-game ranches (no statistically significant trend identified), and (3) non-nuisance wildlife on game ranches (trend approaching statistical significance) across Limpopo Province, South Africa from 2003–2012. Grey shading represents 95% CI; pre-recession years represented by white bars and post-recession years represented by grey bars.



Supporting Information S3.7. Leopard population trends in Limpopo. Camera-trapping protocol, and Bayesian spatially-explicit capture-recapture models used to assess leopard population trends during and after the study period.

## Historical camera-trapping surveys

Limpopo Province comprises some of the most suitable leopard habitat in South Africa (Swanepoel *et al.* 2013). Two regions that have been extensively studied lie within the Vhembe District (Lajuma and adjacent properties, hereafter 'Lajuma'; Lat: -22.97 Long: 29.44) and the Waterberg District (Welgevonden Private Game Reserve; hereafter 'Welgevonden'; Lat: -24.27 Long: 27.80). Lajuma comprises a number of non-protected and protected farms within the Soutpansberg Mountains, whilst Welgevonden is a formally protected private game reserve. Welgevonden is situated within a region of the Waterberg District that has a very high density of game ranches (Exemption Permit Database, LEDET), whereas Lajuma is surrounded by a variety of different land-use types (e.g., livestock and crop farming, game ranches, and private homesteads). Research teams from Lajuma and Welgevonden have published leopard density estimates from camera-trapping surveys conducted during 2008 (Chase Grey, Kent & Hill 2013) and 2009 (Swanepoel, Somers & Dalerum 2015), respectively. Both Lajuma and Welgevonden fall within prime leopard habitat (Swanepoel *et al.* 2013).

## Camera-trapping protocol

Given the importance of Lajuma and Welgevonden for leopard conservation, annual camera-trapping surveys were conducted on Lajuma during 2014 and 2015, and on Welgevonden during 2013, 2014, and 2015 (Table S3.7.1). Paired camera stations (camera model: Panthera V4) were setup at 40–51 locations for a total of 46–56 days per survey. To ensure all individuals within the sampled areas had a probability > 0 of being captured, camera-traps were distributed no further than 3km from one another. To maximize the probability of photographing leopards, camera-traps were placed in high-use areas, such as drainage lines, animal paths, and roads. Camera-traps were mounted on trees or steel poles located 2–4 meters from the focal movement pathway. To reduce false photographic captures, we cleared any vegetation that might obstruct the camera-trap's field of view. Camera-traps were not moved during the surveys. Camera-trap images were cataloged within the camera-trapping database software, Camera Base (Tobler & Powell 2013b). We identified individuals based on their unique pelage patterns within the pattern recognition software, Wild-ID (Bolger *et al.* 2012). In addition, all computer-assisted identifications were manually verified. The sex of each identified individual was determined by the presence, or absence, of testes and other morphological characteristics (e.g., presence of a prominent dewlap, facial scaring, muscle development) (Balme, Hunter & Braczkowski 2012).

### Bayesian spatially-explicit capture-recapture models

We followed the capture re-capture analytical methods, and hierarchical model formulation, described by Goldberg et al. (2015) and Royle et al. (2009). The model relates the observations, $y_{ijk}$, of individual i in trap j during sampling interval k to the latent distribution of activity centers. Observation, $y_{ijk}$, took the value of one for a capture, and zero if not captured, to produce a capture history for all individuals in all traps over all sampling intervals. Multiple detections of the same individual, within the same sampling period, were taken as a single capture. Individuals could be captured on multiple traps during a sampling interval (24 hours). We followed the formulation of the observation process used by Goldberg et al. (2015), Gardner et al. (2010b), and Russell et al. (2012).

Our spatially-explicit capture-recapture models were implemented within a Bayesian framework using data augmentation (Royle & Young 2008; Goldberg *et al.* 2015). Data augmentation adds a sufficiently large number of all-zero capture histories to create a dataset of size M individuals (Goldberg *et al.* 2015). Augmentation was considered large enough when the number of augmented individuals did not truncate the posterior estimates of population size (Proffitt *et al.* 2015; Goldberg *et al.* 2015). Data augmentation in this study varied from 200 to 500. We chose a uniform prior distribution from 0 to M on population size (Goldberg *et al.* 2015). Starting values for parameters were: $\sigma = 1$, $\theta = 0.75$, $\ln(\alpha_0) = 0$, $\beta = 0$, $\Psi = 0$, $\Psi_{sex}$ = proportion of males sampled. We used improper priors $(-\infty,\infty)$ for $\alpha_0$ and all $\beta$ parameters, $(0, \infty)$ for $\sigma$, (0.5, 1) for $\theta$, and (0, 1) for $\Psi$ and $\Psi_{sex}$. Models were fit using Markov chain Monte Carlo (MCMC) methods within R, using the SCRbayes package (available at: https://sites.google.com/site/spatialcapturerecapture/scrbayes-r-package). To account for individual, sex-specific effects, we included a sex covariate within all models. Although cubs (< 12 months old) were occasionally captured on the camera-traps, we only included adults and sub-adults within our analyses. All analyses were run using a statespace of 20 km. Models were run for 30,000 iterations, with a burn-in of 5,000. To reduce autocorrelation, we thinned the MCMC chains by skipping every other iteration, resulting in 12,500 iterations in our posterior sample. We evaluated model goodness of fit using a standard Bayesian P-value approach (Royle *et al.* 2013). Convergence of the MCMC chains were assessed by examining posterior parameter-wise traceplots and histograms. The mean and 95% credibility intervals, for each model parameter, were then computed from these converged samples (Goldberg *et al.* 2015). To enable direct comparisons between historical surveys, and recent surveys, we re-analysed the camera-trapping datasets from Swanepoel et al. (2015) and Chase Grey et al. (2013) using SCRbayes.

### Leopard density estimates

In all cases, assessment of posterior parameter-wise traceplots and histograms indicated that models had converged, and that data augmentation values were adequate (Table S3.7.2). Model fit was excellent, ranging between 0.47–0.52 (Table S3.7.2). Estimates of leopard density suggest that populations have declined over the study period (Fig. S3.7.1). Exposure to increased game ranching densities could explain why Welgevonden’s leopard population has experienced more consistent declines.

Table S3.7.1 Camera-trapping descriptive statistics.

| Survey | Year | Stations* | Trap Nights† | Area‡ | Individuals§ |
|---|---|---|---|---|---|
| Lajuma | 2008¶ | 13 | 819 | 31 | 10 |
| | 2014 | 40 | 1840 | 220 | 31 |
| | 2015 | 40 | 2200 | 220 | 23 |
| Welgevonden | 2009 | 58** | 1297 | 333 | 19 |
| | 2013 | 51 | 2527 | 164 | 17 |
| | 2014 | 40 | 1948 | 228 | 22 |
| | 2015 | 40 | 2240 | 228 | 18 |

* Number of paired camera stations setup during the survey

† Total number of trap nights

‡ Total area covered ($km^2$) by the camera-trapping survey

§ Number of individual leopard (excluding cubs) identified per survey

¶ Data extracted from Chase Grey et al. (2013)

** Swanepoel et al. (2015) used a blocked sampling design by moving 13–15 camera-trap stations over an 18–20 day sampling period

Table S3.7.2 Posterior summaries of model parameters.

| | Survey | Lajuma | | | Welgevonden | | | |
|---|---|---|---|---|---|---|---|---|
| | Year | 2008 | 2014 | 2015 | 2009 | 2013 | 2014 | 2015 |
| Parameter | bsigma | 9.51 (6.00-14.6)* | 5.74 (4.25-7.47) | 4.93 (3.59-6.32) | 5.67 (2.87-9.46) | 3.01 (1.81-4.43) | 2.31 (1.42-3.26) | 1.04 (0.33-2.22) |
| | sigma | 0.23 (0.18-0.29) | 0.30 (0.26-0.34) | 0.32 (0.28-0.37) | 0.31 (0.23-0.42) | 0.42 (0.34-0.53) | 0.47 (0.39-0.59) | 0.75 (0.47-1.22) |
| | bsigma2 | 5.58 (3.06-8.50) | 2.21 (1.14-3.30) | 2.46 (1.56-3.28) | 0.63 (0.14-1.38) | 1.41 (0.99-1.91) | 1.63 (0.77-2.36) | 1.28 (0.86-1.90) |
| | sigma2 | 0.31 (0.24-0.40) | 0.49 (0.39-0.66) | 0.46 (0.39-0.56) | 1.01 (0.60-1.86) | 0.60 (0.51-0.71) | 0.57 (0.46-0.80) | 0.63 (0.51-0.76) |
| | lam0 | 0.11 (0.04-0.29) | 0.07 (0.03-0.14) | 0.07 (0.03-0.12) | 0.03 (0.01-0.07) | 0.02 (0.01-0.04) | 0.04 (0.02-0.06) | 0.03 (0.01-0.09) |
| | psi | 0.58 (0.29-0.94) | 0.67 (0.45-0.91) | 0.42 (0.26-0.62) | 0.59 (0.31-0.93) | 0.36 (0.21-0.58) | 0.59 (0.35-0.89) | 0.43 (0.24-0.71) |
| | psi.sex | 0.22 (0.04-0.54) | 0.10 (0.04-0.21) | 0.22 (0.09-0.42) | 0.06 (0.01-0.17) | 0.25 (0.09-0.48) | 0.36 (0.16-0.63) | 0.68 (0.36-0.91) |
| | Nsuper | 294 (147-481) | 358 (244-484) | 220 (141-324) | 304 (161-482) | 151 (88-239) | 131 (78-197) | 93 (55-153) |
| | theta | 0.70 (0.51-0.98) | 0.69 (0.51-0.97) | 0.59 (0.50-0.87) | 0.81 (0.53-0.99) | 0.91 (0.71-0.99) | 0.58 (0.50-0.83) | 0.88 (0.66-0.99) |
| | GOF† | 0.52 | 0.48 | 0.48 | 0.47 | 0.48 | 0.49 | 0.47 |
| | Density‡ | 0.13 (0.07-0.22) | 0.10 (0.07-0.14) | 0.07 (0.04-0.10) | 0.07 (0.04-0.12) | 0.05 (0.03-0.08) | 0.04 (0.02-0.06) | 0.03 (0.02-0.05) |

* Mean posterior parameter-wise estimate with 95% credibility intervals in parentheses

† Bayesian *P*-value (estimates closer to 0 or 1 indicate poor model fit)

‡ Density estimate (km$^2$)

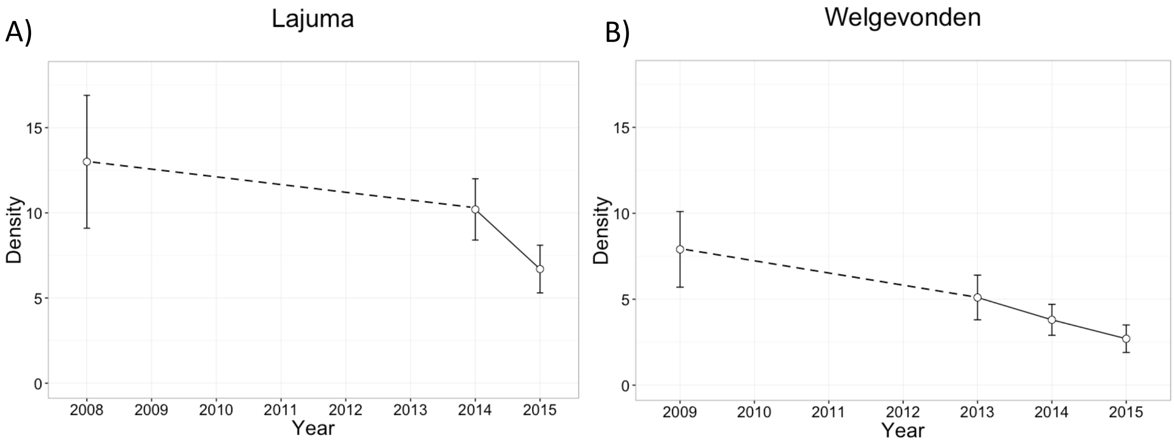


Figure S3.7.1 Leopard population trends in key areas of Limpopo. (a) Leopard population density estimates (leopard/100 km$^2$) for Lajuma, and (b) Welgevonden using spatially-explicit capture-recapture models within a Bayesian framework. The historical datasets from Lajuma (2008) and Welgevonden (2009) were re-analysed using SCRbayes to enable direct comparisons with recent surveys. Error bars represent standard deviation.

## 3.8 TABLES AND FIGURES

Table 3.1. Model descriptions and output. Model outputs include $\beta$ values, standard errors (SE), t-values and significance values (P-value; $\alpha$ at 0.05) for the intercept and coefficients, and the likelihood ratio test statistic ($\chi^2$) and significance value (P-value; $\alpha$ at 0.05) testing each model against their null counterpart.

| | Model description* | $\beta_{intercept}$ | $SE_{intercept}$ | *t*-value | P-value$_{intercept}$ | $\beta_{coefficient}$ | $SE_{coefficient}$ | *t*-value | P-value$_{coefficient}$ | $\chi^2$ | P-value$_{likelihood}$[‡] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| a) | Average price of all game by year[†] | -678.31 | 69.61 | -9.74 | ≤ 0.001 | 0.34 | 0.03 | 9.93 | ≤ 0.001 | 1.75e+11 | ≤ 0.001 |
| b) | Annual turnover of all game by year[†] | -1.048e+03 | 1.04e+02 | -10.05 | ≤ 0.001 | 0.53 | 0.052 | 10.25 | ≤ 0.001 | 6.45e+17 | ≤ 0.001 |
| c) | Number high-value game sold by year[†] | -258.21 | 34.53 | -7.48 | ≤ 0.001 | 0.13 | 0.02 | 7.68 | ≤ 0.001 | 1.18e+06 | ≤ 0.001 |
| d) | Average price of high-value game by year[†] | -681.32 | 69.39 | -9.82 | ≤ 0.001 | 0.35 | 0.03 | 10.00 | ≤ 0.001 | 1.69e+11 | ≤ 0.001 |
| e) | Number common game sold by year[†] | 121.19 | 39.16 | 3.09 | 0.02 | -0.06 | 0.02 | -2.86 | 0.02 | 2.38e+07 | 0.005 |
| f) | Number of ranchers breeding high-value game by year[†] | -2.69e+02 | 7.54 | -35.67 | ≤ 0.001 | 0.14 | 0.004 | 36.20 | ≤ 0.001 | 2757.8 | ≤ 0.001 |
| g) | Number of ranchers using predator-proof fencing by year[†] | -272.13 | 21.79 | -12.48 | ≤ 0.001 | 0.14 | 0.01 | 12.64 | ≤ 0.001 | 999.31 | ≤ 0.001 |
| h) | Permit applications by game ranchers for nuisance wildlife by year | -1.972e+04 | 6356.8 | -3.10 | 0.02 | 9.86 | 3.17 | 3.11 | 0.01 | 8011.7 | 0.002 |
| i) | Permit applications by non-game ranchers for nuisance wildlife by year | -2462.73 | 1597.66 | -1.54 | 0.16 | 1.23 | 0.79 | 1.55 | 0.16 | 124.88 | 0.12 |
| j) | Permit applications by game ranchers for non-nuisance wildlife by year | -1.684e+04 | 8076.55 | -2.09 | 0.07 | 8.42 | 4.02 | 2.09 | 0.07 | 5854.8 | 0.04 |
| k) | Relationship between nuisance wildlife permit applications and the adoption of high-value game breeding | 23.49 | 8.00 | 2.94 | 0.02 | 0.29 | 0.09 | 2.89 | 0.02 | 1414.7 | 0.004 |
| l) | Relationship between nuisance wildlife permit applications and the adoption of predator-proof fencing | 15.76 | 5.37 | 2.93 | 0.02 | 0.16 | 0.07 | 2.38 | 0.05 | 431.85 | 0.02 |

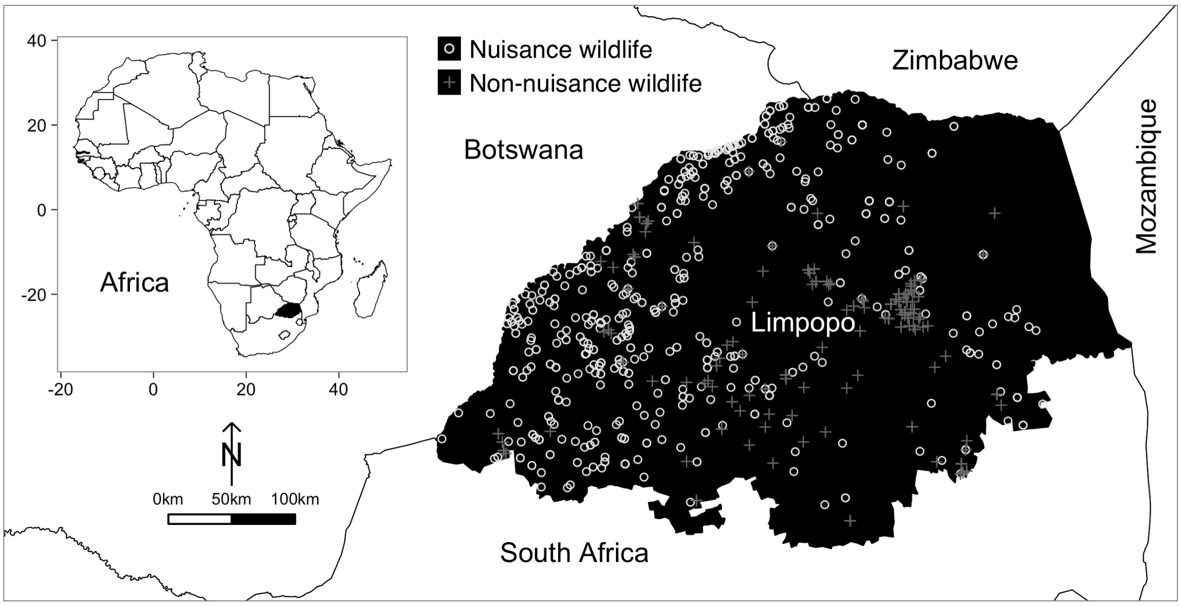


Figure 3.1. Location of the study area situated between northern South Africa, Botswana, Zimbabwe, and Mozambique. White circles and grey crosses represent permit applications for nuisance wildlife and non-nuisance wildlife, respectively. Inset represents the location of the study area within Africa.

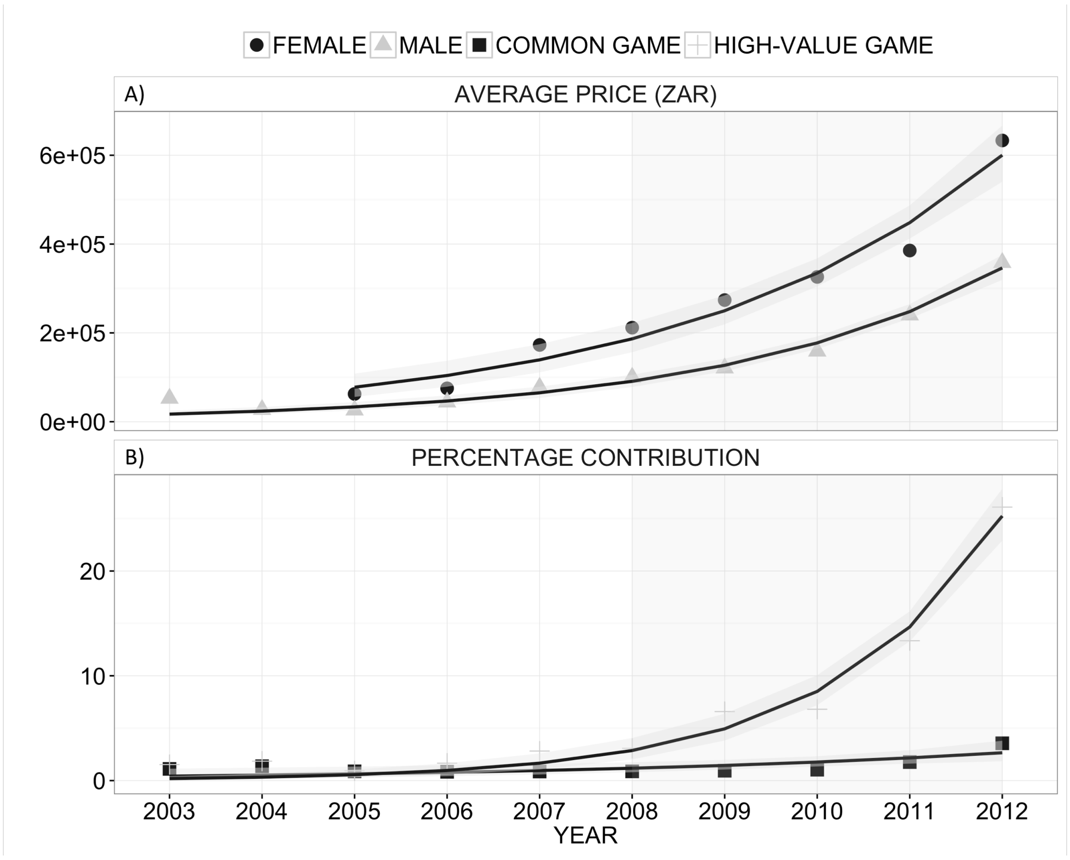


Figure 3.2. High-value game breeding and its economic contribution to Limpopo's economy. (a) Average price (ZAR) of high-value game, categorized by sex (higher price of females emphasizes the importance of breeding), and (b) high-value game breeding's percentage contribution to agricultural gross domestic product in Limpopo Province, South Africa from 2003–2012 (Grey shading represents 95% CI; pre-recession years represented by white bars and post-recession years represented by grey bars).

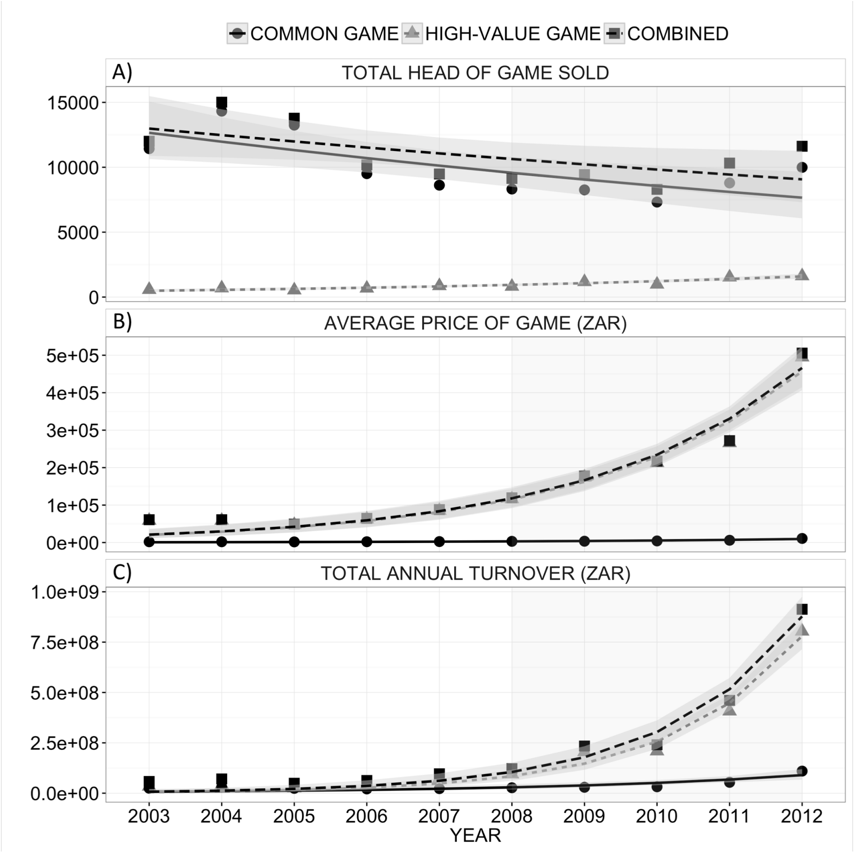


Figure 3.3. Growth in Limpopo's game ranching industry. Game auction data for high-value game, common game, and all game breeds combined from 2003–2012; categorized into (a) total head of game sold, (b) average price of game (ZAR), and (c) total annual turnover (ZAR), for Limpopo Province, South Africa (Grey shading represents 95% CI; pre-recession years represented by white bars and post-recession years represented by grey bars).

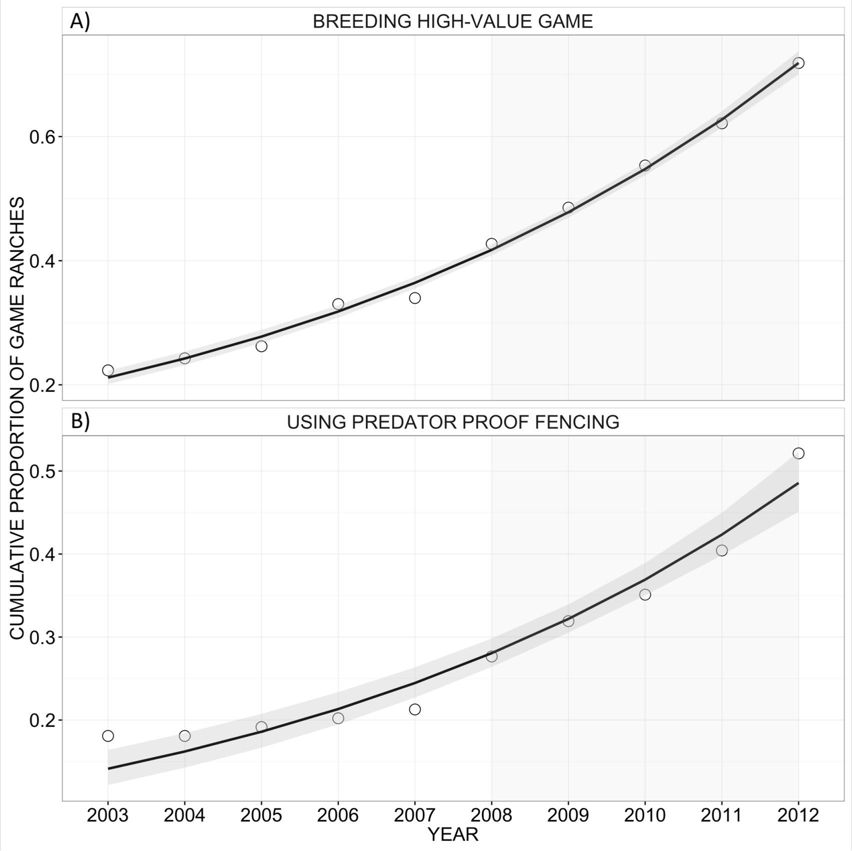


Figure 3.4. High-value game breeding and the adoption of predator-proof fencing. Cumulative proportion of game ranches (a) breeding high-value game, and (b) using predator-proof fencing to protect their game in Limpopo Province, South Africa from 2003–2012 (Grey shading represents 95% CI; pre-recession years represented by white bars and post-recession years represented by grey bars).

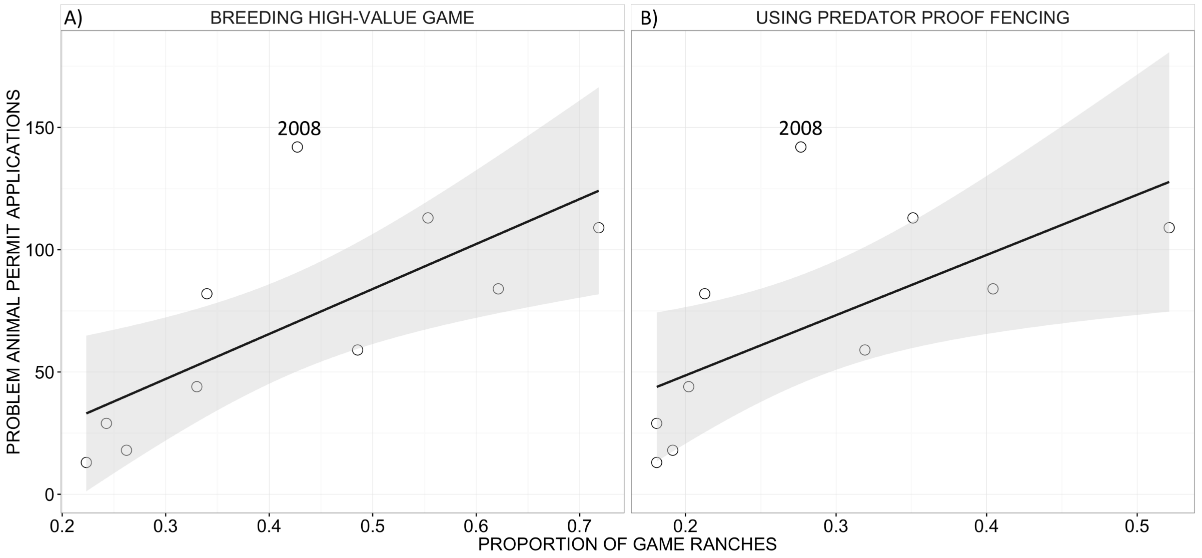


Figure 3.5. Legal destruction of nuisance wildlife and the adoption of game breeding practices. (a) Breeding of high-value game, and (b) using predator-proof fencing (Grey shading represents 95% CI; outlier represents the economic recession of 2008).

# CHAPTER 4 – Cats, connectivity and conservation: incorporating datasets and integrating scales for wildlife management

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## 4.1 ABSTRACT

Understanding resource selection, and quantifying habitat connectivity, are fundamental to conservation planning for both land-use and species management plans. However, datasets available to management authorities for resource selection and connectivity analyses are often highly limited and fragmentary. As a result, measuring connectivity is challenging, and often poorly integrated within conservation planning and wildlife management. To exacerbate the challenge, scale dependent resource use makes inference across scales problematic, resource use is often modelled in areas where the species is not present, and connectivity is typically measured using a source-to-sink approach, erroneously assuming animals possess predefined destinations.

Here, we used a large carnivore, the leopard *Panthera pardus*, to characterise resource use and landscape connectivity across a vast, biodiverse region of southern Africa. Using a range of datasets to counter data deficiencies inherent in carnivore management, we overcame methodological limitations by employing occupancy modelling and resource selection functions across three orders of selection, and estimated landscape-scale habitat connectivity—independent of *a priori* source and sink locations—using circuit theory. We evaluated whether occupancy modelling on its own was capable of accurately informing

habitat connectivity, and identified conservation priorities necessary for applied management.

We detected markedly different scale dependent relationships across all selection orders. Our multi-data, multi-scale approach accurately predicted resource use across multiple scales and demonstrates how management authorities can more suitably utilise fragmentary datasets. We further developed an unbiased landscape-scale depiction of habitat connectivity, and identified key linkages in need of targeted management. We did not find support for the use of occupancy modelling as a proxy for landscape-scale habitat connectivity and further caution its use within a management context.

*Synthesis and applications*. Management authorities routinely collect fragmentary datasets (e.g., mortality data, permit data, sightings data) but infrequently aggregate these data into a single framework to inform management and policy. The loss of connectivity represents a major threat to global biodiversity. We therefore present a robust approach, and subsequent connectivity metrics, optimized for both finer- and coarser-scale management objectives necessary for effective land-use planning and applied wildlife management.

## 4.2 INTRODUCTION

Habitat loss, fragmentation, and degradation are primary causes of global biodiversity loss (Fahrig 2003). Habitat connectivity confers ecosystems with greater resilience towards disturbance (Olds *et al.* 2012), and ultimately facilitates species persistence (Doerr, Barrett & Doerr 2010). Conservation of connectivity has thus become a well-established concept (Zeller, McGarigal & Whiteley 2012), which seeks to maintain or restore genetic exchange between populations (Stockwell, Hendry & Kinnison 2003), thus reducing levels of inbreeding and genetic drift (Soulè & Mills 1998), and provides opportunities for mitigating the negative effects of environmental and demographic stochasticity in a changing world (Hodgson *et al.* 2009). Although globally recognised, connectivity is often poorly considered, or simply does not feature, within wildlife management. As a fundamental component of connectivity conservation, practitioners must identify resources within habitats that facilitate species movement and persistence. Several methods are available to model resource selection and connectivity (Zeller, McGarigal & Whiteley 2012); however, none are without limitations. First, resource selection is scale dependent, such that inference at one scale may not adequately explain resource use at another (Boyce 2006). Second, resource selection within a used-available design is constrained by an ‘asymmetry of errors’ (Boyce 2006), where presence data are observed and known with certainty, but absence data are less certain and often randomly assumed (MacKenzie *et al.* 2006). Third, connectivity is often modelled using a source-to-sink approach (McRae *et al.* 2008), which assumes that animals have a predefined destination (Koen *et al.* 2014). To overcome the constraints of scale dependency, resource selection can be integrated across multiple scales (DeCesare *et al.* 2012; Martin *et al.* 2012); whilst occupancy modelling may be used to account for imperfect detection and more accurately capture resource use at appropriate scales (Gu & Swihart 2004). Similarly, to overcome source-to-sink limitations, connectivity can be mapped across the landscape—irrespective of predefined destination locations—using unbiased spatial techniques (Koen *et al.* 2014).

Here, we use a wide-ranging large carnivore, the leopard *Panthera pardus*, as a model species to estimate resource use and landscape connectivity across leopard range in Limpopo Province, South Africa (hereafter ‘Limpopo’). Leopards are long distance dispersers (Fattebert *et al.* 2015). Their high vagility, and ecological and economic significance (Dalerum *et al.* 2008; Lindsey *et al.* 2012; Maciejewski & Kerley 2014) make leopards an ideal candidate species to identify landscape-scale conservation priorities. Using a range of techniques that overcome the limitations mentioned above, we estimated leopard resource selection across three orders of scale (Meyer & Thuiller 2006): $S_1$, first-order population-level selection across the study area; $S_2$, second-order landscape-level selection across key leopard areas; and $S_3$, third-order individual-level selection across individual home ranges. Specifically, by using occupancy modelling to infer probable locations that are available to leopards across the broader landscape ($S_1$), and resource selection functions (RSFs) to link finer-scaled habitat relationships ($S_2$ and $S_3$), we produce a scale-integrated description of leopard resource use. We use this to develop an unbiased landscape-scale representation of leopard habitat connectivity using circuit theory to identify critical movement pathways across the region (McRae *et al.* 2008). Since broad-scale occupancy data can be conveniently and cheaply collected using questionnaire surveys (Zeller *et al.* 2011), we evaluate whether occupancy modelling on its own is capable of accurately informing habitat connectivity (as derived from circuit theory); with the intention of providing a simple method of incorporating both occupancy and connectivity analyses under a single framework. Finally, we show how our multi-scale approach can be used to identify conservation priorities. Our results provide an unbiased landscape-scale depiction of leopard resource use and connectivity optimized for both finer- and coarser-scaled management objectives applicable for large carnivore conservation and land-use planning more generally.

## 4.3 METHODOLOGY

### 4.3.1 Study area

Limpopo (ca. 125,977 km$^2$; Fig. 4.1) is rich in biodiversity and comprises the largest proportion of suitable leopard habitat in South Africa (Swanepoel *et al.* 2013). A number of formally protected areas occur throughout Limpopo, the most significant being the Kruger National Park (KNP). KNP represents an important source population for leopards within the study area, and is largely unaffected by human-mediated disturbance (Bailey 2005). Outside of KNP, leopards in Limpopo—and South Africa more generally—are managed within geographical catchments representing leopard management units (LMUs). The primary carnivore management practices in Limpopo (i.e., trophy hunting and problem animal control) are strictly designated within LMUs (Pitman *et al.* 2015).

### 4.3.2 First-order ($S_1$) scale of selection

In order to delineate leopard distribution at the broadest scale, we developed a multi-season occupancy model using questionnaire surveys (Zeller *et al.* 2011). The study area (Limpopo and buffer zone; Fig. 4.1) was divided into 596 sampling cells (20 x 20 km). A random stratified sampling approach was used to select a subset of sampling cells to conduct interviews with local inhabitants across Limpopo (Supporting Information S4.2). Respondents acted as surveyors within their 'area of knowledge' defined by a single or group of sampling cells, where each interview from the same sampling cell was considered a separate replicate (Zeller *et al.* 2011). To avoid including residents that spent very little time on their properties, interviews specifically targeted individuals who were resident within their 'area of knowledge' at least twice per month for a minimum of one year. Detections comprised a direct sighting of a leopard or direct observation of sign (e.g., tracks, scat, vocalisations or cached kill). To assess the credibility of each respondent, we asked them to identify photographs of four local species and the tracks of five local species (Supporting Information S4.2). If a respondent was considered non-credible by failing to correctly identify leopard during the vetting process, their data were excluded from all analyses. Surveys were conducted within 98 sampling cells during November 2013 (n = 1 024 respondents). In November 2014 (n = 736) and November 2015 (n = 560), the same respondents were contacted via telephone to conduct the questionnaire verbally. Respondent attrition across years was due to death, change of contact details or residency. A further ground survey was conducted during November 2015 to increase respondent sample size (n = 599 additional respondents) across a randomly stratified subset of sampling cells (n = 55). The distribution of $S_1$ data can be visualised in Supporting Information S4.3.

For multi-season occupancy analyses, we used the package *unmarked* (Fiske & Chandler 2011) within the R statistical environment (R Core Team 2016). Interview responses resulted in detection/non-detection matrices, with a maximum of 40 replicates per sampling cell. Due to potential fluxes in leopard occupancy over the sampling intervals, the assumption of population closure was violated (MacKenzie *et al.* 2006), which changed the occupancy parameter ($\psi$) from 'proportion of area occupied' to 'proportion of area used'. This new interpretation was sufficient to meet our goals, since we were interested in the use of sampling cells, rather than occupation of them (Zeller *et al.* 2011). We used a suite of standardised (mean = 0; standard deviation = 1) resource variables expected to influence leopard distribution (Supporting Information S4.1), and extracted mean values for each resource variable across each sampling cell. Multi-season occupancy modelling seeks to estimate probabilities of occupancy, detection ($p$), colonization ($\gamma$) and extinction ($\epsilon$). We modelled each component (i.e., $\psi, p, \gamma, \epsilon$) as functions of resource variables using logit link functions (MacKenzie *et al.* 2006) by employing a sampling design whereby surveyors (i.e., respondents) visit a sample of $M$ sampling cells and record the binary response $Y_{ij}$ of species detection ($Y = 1$) or non-detection ($Y = 0$) during $j = 1, \ldots, J_i$ visits to the *i*th site during a season (MacKenzie *et al.* 2002). We fitted models with increasing complexity and used Akaike's Information Criterion (AIC) for model selection (Burnham & Anderson 2002). Within each model component we introduced resource variables in a fixed sequence. On identifying a preferred model, and using a backwards stepwise approach, we tried all possible single-term deletions and retained the most parsimonious models (Kéry, Guillera-Arroita & Lahoz-Monfort 2013). We retained non-significant variables within candidate models if they increased parsimony and were ecologically justified. Model-averaging was applied to the most supported models ($\Delta$AIC ≤ 2). The final averaged model was used to predict $\psi$ for each sampling cell across the study area, and was used to delineate available habitat in our $S_2$ RSF.

### 4.3.3 Second- ($S_2$) and third-order ($S_3$) scale of selection

In order to assess leopard resource use at an intermediate scale, $S_2$ datasets were collected from 2000–2015 and comprised published (n = 580 locations) (Swanepoel, Somers & Dalerum 2015) and unpublished camera-trapping studies (n = 1 745 locations; R Pitman/Panthera, unpublished data), expert sightings data (n = 1 384 locations) (Pitman *et al.* 2013b), and leopard mortality data (n = 1 176 locations) (Pitman *et al.* 2015). We randomly distributed an equal number of available locations across the study area, but excluded any areas where $\psi$ was within the lower 25th percentile, as described by our occupancy model. Excluding regions within the lower 25th percentile effectively refined our approach at the landscape-level ($S_2$), and allowed for the exclusion of areas mostly unoccupied by leopards. Although a 25th percentile threshold could be considered arbitrary, this cut-off adequately depicted leopard exclusion areas suggested by previous research (Swanepoel *et al.* 2013).

Leopard resource use at the finest scale (i.e., home ranges) was assessed by collating a range of $S_3$ datasets comprising global positioning system (GPS) collar data and expert long-term sightings data of known individuals from 2004–2015. GPS collar data from eighteen adult leopards were obtained from provincial research surveys (n = 2 leopards; North West Parks and Tourism Board), published studies (n = 8 leopards) (Swanepoel, Dalerum & van Hoven 2010; Pitman, Swanepoel & Ramsay 2012; Pitman *et al.* 2013b; Swanepoel *et al.* 2014b), and unpublished research (n = 8 leopards; Primate and Predator Project). GPS location accuracy metrics (e.g., dilution of precision) were not recorded. All collars acquired a GPS location fix ≥ 4 times per day over the duration of each collar's lifespan (n = 24 027 locations). The GPS collar dataset was filtered by removing any erroneous locations that were beyond the possible range of the study animals (D'Eon *et al.* 2002). Long-term sightings data of known adult individuals were compiled from the Sabi Sands Game Reserve (SSGR; n = 17 942 locations; 62 individuals). Whilst traversing all habitat types within SSGR, field guides are required to record daily leopard sightings, resulting in comprehensive datasets for each known individual (Balme *et al.* 2012). We generated 95% fixed-kernel home ranges for both

GPS collared and resighted individuals (using the reference bandwidth) (Worton 1989). Within each home range we generated an equal number of randomly distributed locations representing available locations.

Using the same resource variables as $S_1$ (Supporting Information S4.1), we extracted mean values for each resource variable using varying buffer radii (m) for each leopard location. This approach was taken as large carnivore resource use is scale dependent and suggests that an optimum predictive radius exists at each order of selection (DeCesare *et al.* 2012; Martin *et al.* 2012). Buffer radii for $S_2$ models comprised 250–1000 m (at 250 m increments), 1000–3000 m (at 500 m increments), and 3000–7000 (at 1000 m increments). Buffer radii for $S_3$ models comprised 50–200 m (at 50 m increments) and 300 m. Buffer radii for $S_2$ and $S_3$ models were determined after accounting for computational efficiency and preliminary assessments. We used fixed-effects logistic regression to compare resource values of used and available locations for $S_2$ scale of selection (i.e., modelling across populations), and mixed-effects logistic regression for $S_3$ scale of selection (fitting leopard individual identities as a random intercept for $S_3$, and thus accounting for correlation and unequal sample sizes) (Gillies *et al.* 2006; Fieberg *et al.* 2010). Correlated resource variables ($|r| > 0.7$) were removed, whilst retaining resource variables that produced the lowest AIC values. $S_2$ and $S_3$ datasets were randomly subset into 80% training and 20% testing datasets to enable internal and external model validation (Boyce *et al.* 2002). Using the training dataset, we ran a suite of models for each order of selection, using resource variables at varying radii. We employed an exhaustive screening approach and ranked candidate models according to AIC. We selected the most parsimonious models, using a single optimum radius for each order of selection, and if necessary, applied model-averaging to the most supported models ($\Delta$AIC ≤ 2) using R package *glmulti* (Calcagno & de Mazancourt 2010). The distribution of $S_2$ and $S_3$ datasets can be visualised in Supporting Information S4.3.

### 4.3.4 Scale-integrated habitat mapping

The used-available designs of $S_2$ and $S_3$ models generated RSFs that are proportional to the probability of use (Manly *et al.* 2002; DeCesare *et al.* 2012). Using a 30 x 30 m resolution, per pixel predicted values ($w_{js}$) were spatially mapped across the study area. We estimated $S_2$ and $S_3$ RSF predicted values (Manly *et al.* 2002), as

$$w_{js}(x) = exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k) \tag{1}$$

We applied a linear stretch to rescale $S_2$ and $S_3$ RSF predicted values between 0 and 1 (Johnson, Seip & Boyce 2004), as

$$\widehat{w}_{js} = \left(\frac{w_{js}(x) - w_{min}}{w_{max} - w_{min}}\right). \tag{2}$$

To develop a scale-integrated RSF (SRSF) across the study area representing relative probability of use for a given pixel ($w_{SRSF}$), we multiplied each scale's probabilities (*P*) (Johnson, Seip & Boyce 2004; DeCesare *et al.* 2012), as

$$w_{SRSF} = P(S_2) \times P(S_3) \tag{3}$$

Finally, we applied a linear stretch to rescale the resulting SRSF between 0 and 1 using Eq. 2.

### 4.3.5 Multi-scale model validation

We used model validation procedures to examine the predictive capacity of single scale RSFs ($S_2$ and $S_3$) and scale-integrated (SRSF) models. We reclassified models into 10 equal area bins using percentile breaks at 10% intervals (Boyce *et al.* 2002). Withheld testing datasets were used as validation points for each scale separately (i.e., independent and partially-dependent validation). We then projected validation points across the landscape, and assigned each a bin value according to the underlying reclassified landscape. We used Spearman's rank correlation to compare the frequencies of validation points in each bin to each RSF's bin rank (Boyce *et al.* 2002). A strongly predictive model will have a high positive correlation, indicating a greater number of locations in probability bins that approach 1 (Johnson, Seip & Boyce 2004).

### 4.3.6 Connectivity mapping

We combined our SRSF with circuit theory to explore habitat connectivity using Circuitscape v.4.0.5 (McRae *et al.* 2008). We chose circuit theory over other commonly used connectivity methods (e.g., least-cost path) since circuit theory models movement ecology via random walk pathways across all available movement possibilities (McRae *et al.* 2008). The SRSF was used as an index of conductance, where all cells are defined by networks of electrical nodes connected by resistors (see McRae *et al.* 2008 for a review). Random-walk conductance modelling is analogous to habitat permeability (i.e., movement potential of an organism across the landscape), and is directly related to the likelihood of a 'walker' choosing to move through a cell, relative to other cells available to it (McRae *et al.* 2008). By predicting net movement probabilities through electrical nodes, current flow (i.e., permeability) can be used to identify core use areas, habitat connectivity and key movement pathways (McRae *et al.* 2008). Connectivity modelling is typically conducted between habitat patches, or between *a priori* source and sink locations. However, this is a key limitation, as animals often lack a predefined destination (Koen *et al.* 2014). To overcome this constraint, we developed a landscape-scale permeability map that is independent of *a priori* source or destination locations by randomly placing regularly distanced nodes (hereafter 'random nodes') around the 50 km buffer perimeter (Koen *et al.* 2014). Connectivity was then measured across the landscape, from one random node to another, in a pairwise fashion. To identify the optimum number of random nodes required to generate an unbiased landscape-scale permeability map, we conducted a sensitivity analysis using 10 to 300 random nodes at intervals of 10. Current flow was modelled across all random nodes to generate 30 permeability maps. If our estimates of permeability were independent of node placement and quantity, we should expect little variation in the spatial distribution of current flow as the number of random nodes increases (Koen *et al.* 2014). To test this prediction, we removed the buffer region and distributed 100,000 random locations across Limpopo. The buffer region was removed prior to testing because its inclusion would result in a biased estimate resulting from overestimated landscape conductivity at the periphery (Koen *et al.* 2010). We compared estimates extracted from each permeability map (i.e., 10–290 node maps) against estimates from the full permeability map (developed with 300 random nodes) by evaluating Pearson correlation coefficients. An optimum number of random nodes is only deemed suitable once an asymptote in correlation coefficients is reached (Koen *et al.* 2014). We applied a linear stretch to rescale the final permeability map between 0 and 1 using Eq. 2.

### 4.3.7 Management implications

To assess habitat permeability within LMUs (leopard management units; n = 207), we compared LMU current density estimates (i.e., flow of current km$^{-2}$; $\frac{total\ current\ flow_{LMU_i}}{total\ area_{LMU_i}}$) across Limpopo (excluding KNP; n = 180) against current density estimates from LMUs across KNP (n = 27) using a two-sampled t-test. Using the mean current density of LMUs within KNP as an optimum baseline $(\mathrm{KNP}_{base})$, we categorized the permeability potential for LMUs across Limpopo as either below-optimum $(< \mathrm{KNP}_{base})$ or above-optimum $(> \mathrm{KNP}_{base})$. Given the size, low degree of human disturbance, and optimal habitat (Swanepoel *et al.* 2013), KNP represents an ideal baseline on which to gauge the permeability potential of LMUs across Limpopo. Capacity for species and environmental monitoring is often a limiting factor; therefore, to test whether broad-scale occupancy modelling ($S_1$) could be used as a proxy for landscape permeability, we ranked $\psi$ estimates and compared them against mean current density estimates within each $S_1$ sampling cell using Spearman's rank correlation.

## 4.4 RESULTS

### 4.4.1 Modelling resource use at $S_1$

We recorded 312, 150 and 138 leopard detections during 2013, 2014 and 2015, respectively. Four top models qualified for model averaging (Table 4.1), whilst four resource variables were removed due to collinearity (EVI, NDVI, NPP, and terrain ruggedness). Leopards selected, and were more likely detected, in drier regions further from major road networks. Although the parameters were likely non-informative (95% CI overlapped with zero), leopards appeared to avoid areas with denser vegetation, but selected areas with more people. We assumed these two variables were more likely associated with detection probability—particularly selection for areas closer to people, since this might represent a bias in our survey approach. However, we found this not to be the case as these models were outperformed by more parsimonious models (Table 4.1). Both $\gamma$ and $\epsilon$ were held constant, as candidate models did not improve when resource variables were included. The resulting predictive map ($\psi$, Fig. 4.2a) agreed with previously published research (Swanepoel *et al.* 2013).

### 4.4.2 Modelling resource use at $S_2$ and $S_3$

Two vegetative resource variables (NPP and NDVI) were removed due to collinearity at both orders. Leopard selection response to features were strongest when resource variables were measured at radii of 7000 m (Fig. 4.3a) and 100 m (Fig. 4.3b) for $S_2$ and $S_3$ scales of selection, respectively. $S_2$ scale of selection, model-averaging comprised two top models. Leopards favoured areas close to riverine and protected areas that were less rugged and at higher elevations, but further from major road networks. Tree canopy cover and EVI were all positively selected for, whereas human population density was negatively selected for (Table 4.2). $S_3$ scale of selection comprised two top models. Leopards favoured riverine areas of high vegetative productivity (EVI and tree canopy cover) and ruggedness, but in regions of lower precipitation (Table 4.2). Model validation at $S_2$ (partially-dependent testing dataset: $r_s$ = 0.99, $P < 0.001$; independent testing dataset: $r_s$ = 0.92, $P < 0.001$) and $S_3$ (partially-dependent testing dataset: $r_s$ = 1, $P < 0.001$; independent testing dataset: $r_s$ = 0.92, $P < 0.001$) scales of selection performed well, and similarly for the final SRSF (partially-dependent testing dataset: $r_s$ = 1, $P < 0.001$), suggesting the predictive capacity of all models was very high (Fig. 4.2 b–d).

### 4.4.3 Modelling landscape-scale habitat permeability

Using the final SRSF as an index of conductance (Fig. 4.2d), we developed an unbiased landscape-scale permeability map using ≥200 random nodes (Pearson mean $r_{200\text{–}290\ nodes}$ = 0.89)—note an asymptote is reached by 200 random nodes (Fig. 4.4). As there is no penalty to including too many random nodes (Koen *et al.* 2014), we chose to use the full map for further connectivity assessments (Fig. 4.5a). Leopard habitat permeability was moderate across Limpopo (mean current flow = 0.5 ± 0.001 SE; range: 0–1). Three distinct regions exhibited markedly low habitat permeability (Fig. 4.5a). Current density of LMUs within KNP were significantly higher (mean = 1.7 ± 0.1 km$^{-2}$ SE; $\mathrm{KNP}_{base}$) than LMUs outside of KNP (1.3 ± 0.06 km$^{-2}$ SE; two-sample t-test: $t_{(46)} = 3.6, P < 0.001$). Using $\mathrm{KNP}_{base}$ as an optimum baseline, a total of 51 LMUs (25%; 18,198 km$^2$) were characterized with above-optimal permeability (Fig. 4.5b), whilst the remaining 156 LMUs (75%; 108,983 km$^2$) were characterized with below-optimal permeability (Fig. 4.5b). We detected a weak relationship between ranked $\psi$ estimates and mean current density estimates across $S_1$ sampling cells ($r_s$ = 0.31, $P < 0.001$), suggesting occupancy modelling was a poor predictor of landscape permeability.

## 4.5 DISCUSSION

We integrated across multiple scales of resource selection and generated an unbiased landscape-scale permeability map that was independent of *a priori* source or sink locations. We demonstrated a scale-integration method capable of overcoming scale dependent limitations to accurately predict resource use for an elusive, large carnivore. We compiled a range of datasets to counter the dearth of information often attributed to large carnivore research, which enabled the delineation of broad-scale ($S_1$) leopard distribution, and finer-scaled resource selection ($S_2$ and $S_3$), and identified key variables influencing different scales. Given the wide-ranging dispersal capabilities of leopards, and to facilitate a more informed used-available design, we used occupancy modelling ($S_1$) to delineate areas available to leopards at the intermediate ($S_2$) scale. Occupancy modelling is being increasingly adopted at broad-scales to address species distributions and habitat linkages (Zeller *et al.* 2011; Koen *et al.* 2014); however, although we produced a $\psi$ map that was consistent with previous research from the same region (Swanepoel *et al.* 2013), we did not find support for the use of broad-scale occupancy modelling as a proxy for landscape permeability. This finding suggests that management authorities should exercise caution when attempting to use broad-scale occupancy modelling to infer landscape-scale linkages (Zeller *et al.* 2011). More specifically, we found that leopard habitat permeability across Limpopo is moderate, and identify three key regions that exhibit markedly low permeability. Importantly, the permeability of LMUs across Limpopo are largely below-optimal when compared to prime leopard habitat, which warrants further conservation attention and management intervention.

Obtaining data for the management of elusive animals is challenging and often results in fragmentary datasets (Martin *et al.* 2012). By incorporating multiple datasets across multiple scales, resource selection models can be developed that infer fine-scale spatial relationships represented by the larger population, but which are less prone to spatial bias in resource use typically caused by limited datasets (Martin *et al.* 2012; Elliot *et al.* 2014). Elliot *et al.* (2014) demonstrated the importance of using a range of datasets (i.e., demographic categories) when parameterizing resistance surfaces for connectivity modelling, so as not to produce erroneous conclusions. We too advocate the use of a range of datasets in situations where broad-scale ecological and management questions are being posed for elusive species that cover vast areas (i.e., leopards); particularly since the management of these species are largely characterised by data deficiencies. Our study produced robust estimates of leopard distribution ($\psi$) at the broadest scale, which informed finer-scale RSF analyses (i.e., by excluding areas mostly unoccupied by leopards). Fine-scale resource use is governed by fine-scale resource availability, which is itself governed by broad-scale resource selection (DeCesare *et al.* 2012). This hierarchically-nested relationship has previously been exploited for other large mammals, such as woodland caribou *Rangifer tarandus caribou* (DeCesare *et al.* 2012) and brown bear *Ursus arctos* (DeCesare *et al.* 2012; Martin *et al.* 2012). However, earlier studies relied on limited datasets to delineate population distribution at the broadest scale. This potentially limits the robustness of a used-available study design, as available locations at finer scales might be randomly placed within areas unoccupied by the study species. The elusive nature and low detection rates of large carnivores calls for a more robust framework (Ripple *et al.* 2014), which occupancy modelling may provide.

Patterns of resource use involve balancing the trade-off between the costs of resource acquisition against the benefits of resource use (Brown, Laundré & Gurung 1999). For large carnivores such as the leopard, selection trade-offs exist between prey abundance and catchability (Balme, Hunter & Slotow 2007), and avoidance of intraspecific and interspecific threats (Vanak *et al.* 2013). Depending on the scale, selection trade-offs can act at differing intensities, which can render wildlife-habitat relationships non-informative, resulting in skewed connectivity metrics (Boyce 2006). Here, we demonstrated markedly different scale dependencies for a highly adaptive large carnivore (Hayward *et al.* 2006). Leopard distribution patterns at the broadest scale of selection ($S_1$) were primarily driven by a lack of major road networks. At finer scales ($S_2$ and $S_3$), leopard resource use was governed by three factors; avoidance of anthropogenic disturbance (road networks and people), selection of prey-rich areas (riverine features, proximity to protected areas, high EVI and high precipitation), and selection of rugged areas with sufficient vegetative cover likely to maximise hunting success and minimise kleptoparasitism (Balme, Hunter & Slotow 2007). By integrating across multiple scales of resource selection, we accommodated complex leopard-habitat relationships within a single framework capable of generating accurate predictions of resource use necessary for applied large carnivore management.

Free-ranging wildlife is under significant anthropogenic pressure (Ripple *et al.* 2014; 2015). Land-use practices, in particular, have led to increased fragmentation and human-wildlife conflict (Pitman *et al.* 2016). Habitat connectivity is not only essential to maintain genetic variability (Broquet *et al.* 2010), trophic diversity and ecosystem functions (Olds *et al.* 2012), but also ensures the persistence of free-ranging charismatic species that play an important economic role (Lindsey, Roulet & Romanach 2007). Wildlife management is increasingly focused at the landscape-scale, where connectivity conservation across vast regions are superseding those at smaller scales (Koen *et al.* 2014). Although connectivity is typically modelled using a source-to-sink approach (Zeller, McGarigal & Whiteley 2012), we stress the importance of methodologies that do not rely on *a priori* destination locations. The distribution of wildlife in human dominated landscapes is poorly understood (Koen *et al.* 2014), particularly at finer scales (Boyce 2006). Moreover, knowledge of definitive source and sink locations is severely lacking, even for a large, charismatic species such as the leopard (Pitman *et al.* 2015). Using random nodes placed around the perimeter of the buffered study area, we modelled connectivity across the entire landscape independent of *a priori* source or sink locations. This broader applicability results in landscape permeability maps relevant not only to leopard ecology and management, but also to species at comparable or lower trophic levels reliant on similar habitat types.

Large carnivores have undergone significant range contractions (Ray, Hunter & Zigouris 2005), leading to increased calls for improved management and conservation (Ripple *et al.* 2014). As with wildlife management more generally, large carnivore management is often implemented across discrete geographical units (e.g., wildlife management units, hunting concessions, administrative zones) (Messmer *et al.* 1998). For instance, lions *Panthera leo* are typically managed within hunting concessions (Lindsey, Roulet & Romanach 2007), whilst cougar *Puma concolor* hunting in Utah, USA is managed within geographical watersheds (Stoner *et al.* 2013). Although connectivity is a fundamental component of successful conservation (Zeller, McGarigal & Whiteley 2012), connectivity metrics are infrequently considered within the regulatory processes of many range states. This exclusionary approach is largely down to the difficulty, and high cost, of collecting data of sufficient quality and quantity for connectivity analyses; and often prevents management authorities from incorporating connectivity metrics within wildlife management. Management authorities, however, frequently collect fragmentary, opportunistic datasets such as mortality records, permit records and sightings data (Pitman *et al.* 2015; 2016). As our approach clearly demonstrates, data from these multiple sources (and scales) can be efficiently incorporated into connectivity analyses and applied within a management context. Moreover, since carnivore management is often focused within geographical units (e.g., LMUs), management authorities could efficiently address regions of low connectivity by selectively modifying management practices (e.g., reducing trophy hunting quotas and problem animal control within management units) to mitigate human-mediated pressures. In our case study, we show that three regions in Limpopo exhibit markedly low habitat permeability and warrant urgent conservation attention. For instance, the establishment of conservancies can greatly increase wildlife persistence by linking suitable habitat (Lindsey, Romanach & Davies-Mostert 2009a); therefore, as an alternative to modifying management practices within management units, management authorities could incentivise conservancy establishment across units requiring targeted management. Similarly, community engagement can play an important role in improving perceptions and tolerance of carnivores (Dickman 2010). Community outreach projects could thus be more effectively implemented if management authorities employ a multi-data, multi-scale connectivity approach—as we present here—to identify management units at risk of low permeability. Lastly, environmental impact assessments, which are routinely conducted in the region, could draw on the findings presented in this study; particularly with regard to game ranching practices, which are leading to increased landscape fragmentation through the adoption of heavily fortified predator-proof fencing (Pitman *et al.* 2016). Although our findings focus on a large carnivore across a biodiverse region of southern Africa, they remain easily transferable for the management of other ecologically important species exhibiting wide-ranging dispersal capabilities and diverse habitat requirements.

## 4.6 ACKNOWLEDGEMENTS

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## 4.7 SUPPORTING INFORMATION

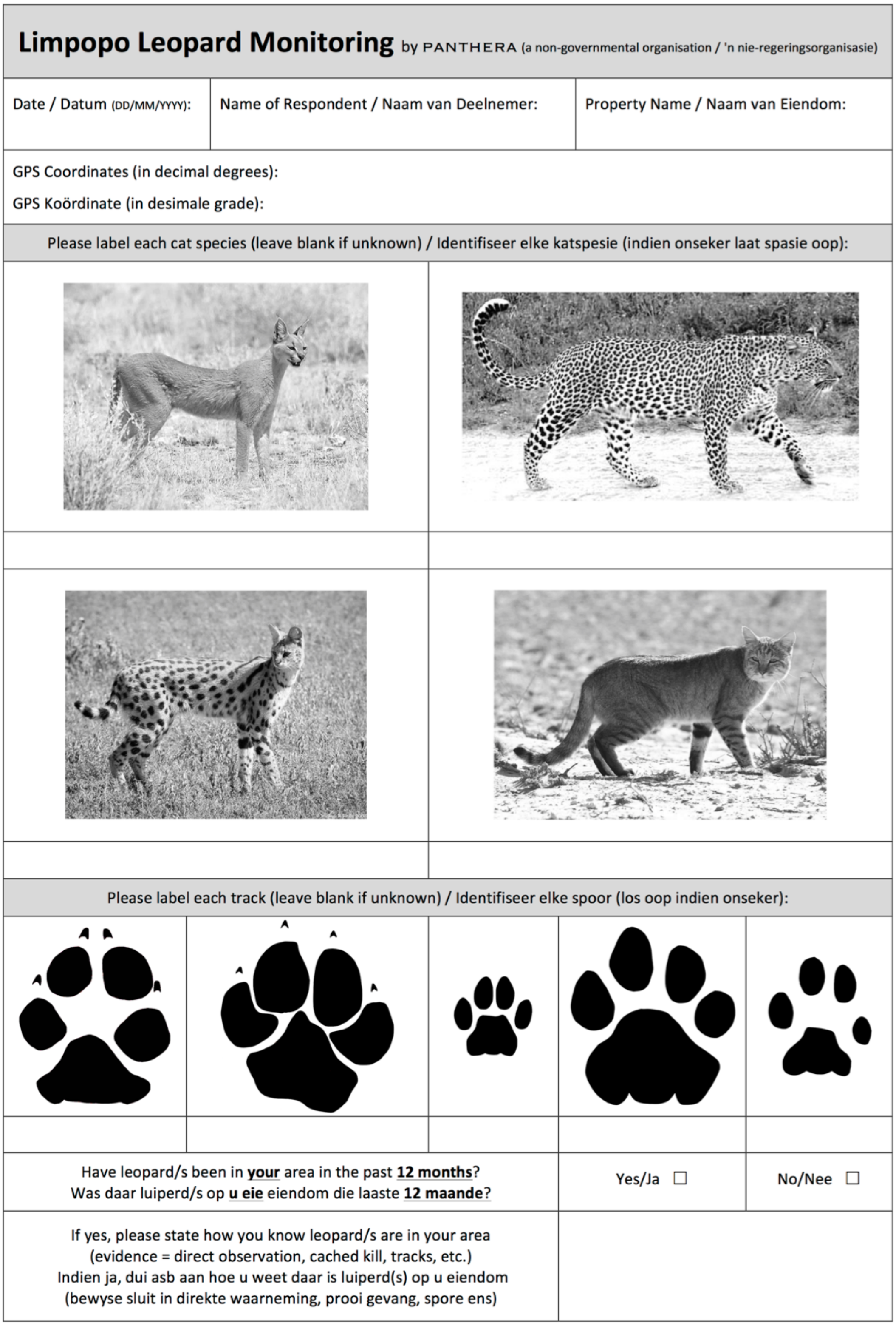
Supporting Information S4.1. Description of resource variables used to model leopard *Panthera pardus* resource selection at first- ($S_1$), second- ($S_2$) and third-order ($S_3$) scales of selection.

| **Resource variable *** | **Rationale** | **Source** |
|---|---|---|
| *Distance* | | |
| Distance to water | Leopard favour areas closer to water where their primary prey species aggregate (Hayward et al. 2006; Balme et al. 2007). | Department of Agriculture, Forestry and Fisheries |
| Distance to major roads | Leopard avoid major road networks, as these networks are typically concentrated in areas densely populated by people (Swanepoel et al. 2013). | Chief Surveyor General (Cadastral Spatial Information, Pretoria) |
| Distance to protected areas | Leopard favour areas closer to protected areas, as these areas represent refuge sites (Swanepoel et al. 2013). | World Database on Protected Areas (IUCN and UNEP-WCMC 2016) |
| *Topographical* | | |
| Elevation | Leopard favour areas of higher elevation as hunting success may be higher (i.e., prey may find it difficult to escape whilst in rocky terrain), and human density is typically lower (Swanepoel et al. 2013). | SRTM30 (http://srtm.usgs.gov/) |
| Terrain ruggedness | Leopard favour areas of increased ruggedness as hunting success may be higher (i.e., prey may find it difficult to escape whilst in rugged terrain) (Fattebert et al. 2015). | SRTM30 (http://srtm.usgs.gov/) |
| *Vegetative*† | | |
| Net primary productivity | Leopard favour areas with greater vegetative productivity as these areas are typically prey rich (Swanepoel et al. 2013; Farhadinia et al. 2015). | MOD17A3 (https://lpdaac.usgs.gov/products/modis_products_table) |
| Normalized difference vegetation index | Leopard favour areas with a high normalized difference vegetation index as these areas are typically prey rich (Swanepoel et al. 2013). | Landsat 8 (http://landsat.usgs.gov/landsat8.php) |
| Environmental vegetation index | Leopard favour areas with a high environmental vegetation index as these areas are typically prey rich (Fattebert et al. 2015). | MODIS Daily EVI (https://lpdaac.usgs.gov/products/modis_products_table) |
| Tree canopy cover | Leopard favour areas with suitable vegetation cover (e.g., tree cover) as these areas facilitate ambush strategies (i.e., stalking cover), and reduce competition and kleptoparasitism by acting as refuge areas (Balme et al. 2007; Pitman et al. 2012). | Global Forest Change |
| *Climatic* | | |
| Precipitation | Leopard favour areas of high precipitation as these areas are typically prey rich (Farhadinia et al. 2015). | WorldClim (http://www.worldclim.org/) |
| *Anthropogenic* | | |
| Human population density | Leopard avoid areas densely populated by people (Swanepoel et al. 2013). | WorldPop (http://www.worldpop.org.uk/) |

* Resource variables were all continuous and resampled to 30 x 30 m resolution

† Vegetative resource variables represented proxies of prey availability, since a prey abundance metric was not available for the study extent

Supporting Information S4.2. Structured questionnaire survey.



**Limpopo Leopard Monitoring** by PANTHERA (a non-governmental organisation / 'n nie-regeringsorganisasie)

| | | |
|---|---|---|
| Date / Datum (DD/MM/YYYY): | Name of Respondent / Naam van Deelnemer: | Property Name / Naam van Eiendom: |

GPS Coordinates (in decimal degrees):
GPS Koördinate (in desimale grade):

Please label each cat species (leave blank if unknown) / Identifiseer elke katspesie (indien onseker laat spasie oop):

Please label each track (leave blank if unknown) / Identifiseer elke spoor (los oop indien onseker):

| | | |
|---|---|---|
| Have leopard/s been in **your** area in the past **12 months**?<br>Was daar luiperd/s op **u eie** eiendom die laaste **12 maande**? | Yes/Ja ☐ | No/Nee ☐ |

| | |
|---|---|
| If yes, please state how you know leopard/s are in your area<br>(evidence = direct observation, cached kill, tracks, etc.)<br>Indien ja, dui asb aan hoe u weet daar is luiperd(s) op u eiendom<br>(bewyse sluit in direkte waarneming, prooi gevang, spore ens) | |

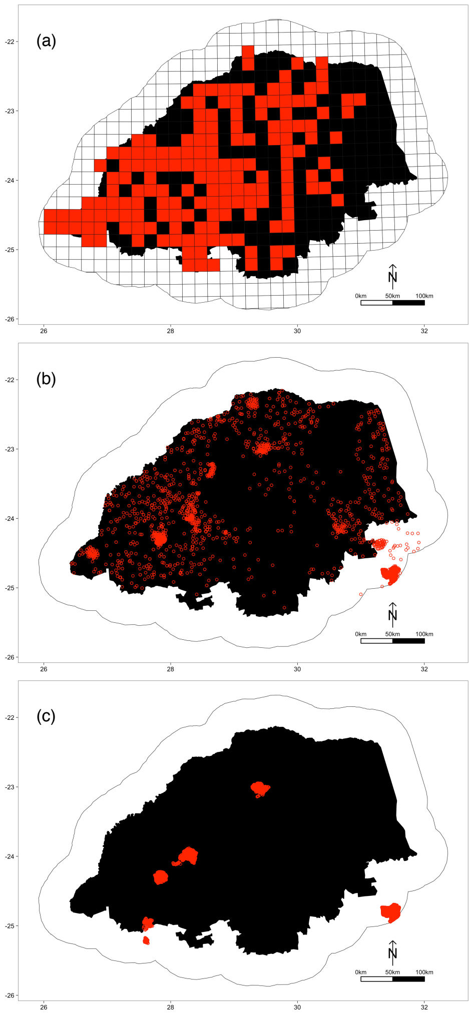
| | | |
|---|---|---|
| If yes, on what date/s did this occur? (MM/YYYY)<br>Indien ja, op watter datum(s) het dit voorgekom (MM/JJJJ) | | |
| If yes, please state the frequency of leopard sightings in your area?<br>Indien ja, hoe gereeld is luiperds/tekens waargeneem op u eiendom? | Rare (once a year)<br>Ongereeld (eenmaal per jaar) | ☐ |
| | Sometimes (once every 6 months)<br>Soms (elke 6 maande) | ☐ |
| | Frequent (once a month or more)<br>Gereeld (eenkeer per maand of meer) | ☐ |
| How long have **you** lived on your property? (months and/or years)<br>Hoe lank woon u al op die huidige eiendom (in maande en/of jare) | | |
| How many months a year do **you** spend on your property?<br>Hoeveel maande per jaar spandeer **uself** op die eiendom? | | |
| As part of an on-going leopard monitoring program, I would kindly like to ask if I could phone you in a year to ask these questions again?<br>As deel van 'n langtermyn moniterings program, wil ek vriendelik versoek dat ek u oor 'n jaar weer mag kontak om dieselfde vraelys te voltooi. | Cellphone/ Selfoon: | |
| | Alt. Cellphone/Selfoon: | |
| | Landline/landlyn: | |

## Thank you for taking part in this survey
## Baie dankie dat u deelgeneem het aan die opname

PANTHERA

| For Official Use Only | | | |
|---|---|---|---|
| Name of Interviewer | | | |
| Time | | Grid Number | |
| Signature | | | |
| Checklist | | | |
| Did you explain that this survey was voluntary? | Yes ☐ No ☐ | | |
| Did you give the respondent a copy of the Informed Consent Document? | Yes ☐ No ☐ | | |
| Do the data qualify for analysis? | Yes ☐ No ☐ | | |
| Are the data captured? | Yes ☐ No ☐ | | |

Supporting Information S4.3. (a) Distribution of datasets across three orders of selection. $S_1$ scale of selection depicted by 400km$^2$ red sampling cells, (b) $S_2$ scale of selection depicted by red point locations, and (c) $S_3$ scale of selection depicted by red point locations used to develop individual leopard home ranges.



# 4.8 TABLES AND FIGURES

## Table 4.1. Top multi-season occupancy models for predicting leopard *Panthera pardus* habitat use ($\psi$; ‘proportion of area used’) from 2013–2015

| Models* | $\Delta$AIC† | AIC‡ | AIC$_w$ | CW¶ | K§ | Coefficients of resource variables | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | $\psi$ ** | | | | | $\gamma$ †† | $\epsilon$ ‡‡ | $p$¶¶ | | |
| | | | | | | Intercept | D.Road | Precip §§ | Canopy §§ | Human §§ | Intercept | Intercept | Intercept | D.Road | Precip |
| $\psi$(D.Road + Precip) $\gamma$(.) $\epsilon$(.) $p$(D.Road + Precip) | 0.0 | 2198 | 0.34 | 0.34 | 8 | -3.4 (1.7) *** | 0.005 (0.001) | -0.002 (0.002) | – | – | -0.598 (0.340) | -0.437 (0.209) | -0.015 (0.280) | 8.0E-04 (9.9E-05) | -0.004 (4.6E-04) |
| $\psi$(D.Road) $\gamma$(.) $\epsilon$(.) $p$(D.Road + Precip) | 0.3 | 2199 | 0.63 | 0.63 | 7 | -5.0 (1.4) | 0.005 (0.001) | – | – | – | -0.067 (0.354) | -0.514 (0.213) | -0.039 (0.275) | 8.0E-04 (9.8E-05) | -0.004 (4.6E-04) |
| $\psi$(D.Road + Canopy) $\gamma$(.) $\epsilon$(.) $p$(D.Road + Precip) | 0.7 | 2199 | 0.87 | 0.87 | 8 | -4.3 (1.3) | 0.005 (0.001) | – | -0.065 (0.061) | – | -0.650 (0.346) | -0.472 (0.211) | -0.116 (0.275) | 8.0E-04 (9.8E-05) | -0.003 (4.5E-04) |
| $\psi$(D.Road + Precip +Human) $\gamma$(.) $\epsilon$(.) $p$(D.Road + Precip) | 2.0 | 2200 | 1.00 | 1.00 | 9 | -3.4 (1.7) | 0.005 (0.001) | -0.002 (0.002) | – | 0.015 (9.179) | -0.598 (0.340) | -0.437 (0.209) | -0.015 (0.281) | 8.0E-04 (9.9E-05) | -0.004 (4.6E-04) |

* Top models were averaged using R package *unmarked* (Fiske & Chandler 2011)

† Delta AIC

‡ Akaike’s Information Criterion (Burnham & Anderson 2002)

¶ Cumulative AIC weights

§ Number of parameters in each model

** Probability of occupancy, interpreted in this study as ‘probability of habitat use’

†† Probability of colonisation

‡‡ Probability of extinction

¶¶ Probability of detection

§§ Non-informative parameters (95% CI overlapping with zero)

*** Standard error given in parentheses

Table 4.2. Fixed- ($S_2$) and mixed-effects ($S_3$) logistic regression coefficients from averaged models ($\Delta$AIC ≤ 2)

| Coefficient* | $\beta$ | SE | $z$ | *P* | *RI*† |
|---|---|---|---|---|---|
| $S_2$ | | | | | |
| Intercept | -1.68 | 0.09 | 19.78 | <0.001 | 1.00 |
| d.water.7000 | -0.63 | 0.08 | 7.61 | <0.001 | 1.00 |
| d.roads.7000 | 0.59 | 0.12 | 5.11 | <0.001 | 1.00 |
| human.7000 | -6.50 | 0.28 | 23.03 | <0.001 | 1.00 |
| evi.7000 | 1.27 | 0.08 | 15.65 | <0.001 | 1.00 |
| elevation.7000 | 0.22 | 0.05 | 5.01 | <0.001 | 1.00 |
| t.rugged.7000 | -0.52 | 0.06 | 8.38 | <0.001 | 1.00 |
| t.canopy.7000 | 0.19 | 0.08 | 2.38 | 0.02 | 1.00 |
| d.PA.7000 | -1.82 | 0.13 | 13.73 | <0.001 | 1.00 |
| precip.7000 | 0.01 | 0.04 | 0.21 | 0.84 | 0.28 |
| $S_3$ | | | | | |
| Intercept | -0.57 | 0.08 | 6.81 | <0.001 | 1.00 |
| d.water.100 | -0.62 | 0.04 | 16.61 | <0.001 | 1.00 |
| precip.100 | -0.22 | 0.02 | 9.05 | <0.001 | 1.00 |
| evi.100 | 0.17 | 0.02 | 9.95 | <0.001 | 1.00 |
| t.rugged.100 | 0.12 | 0.01 | 14.72 | <0.001 | 1.00 |
| t.canopy.100 | 0.15 | 0.02 | 10.11 | <0.001 | 1.00 |
| dpa.100 | 0.12 | 0.14 | 0.84 | 0.40 | 0.57 |

* Resource variable prefixes: d.water – distance to water; d.roads – distance to roads; human – human population density; evi – environmental vegetation index; elevation – altitude; t.rugged – terrain ruggedness; t.canopy – tree canopy cover; d.PA – distance to protected area; precip – precipitation

† AIC weights of relative variable importance

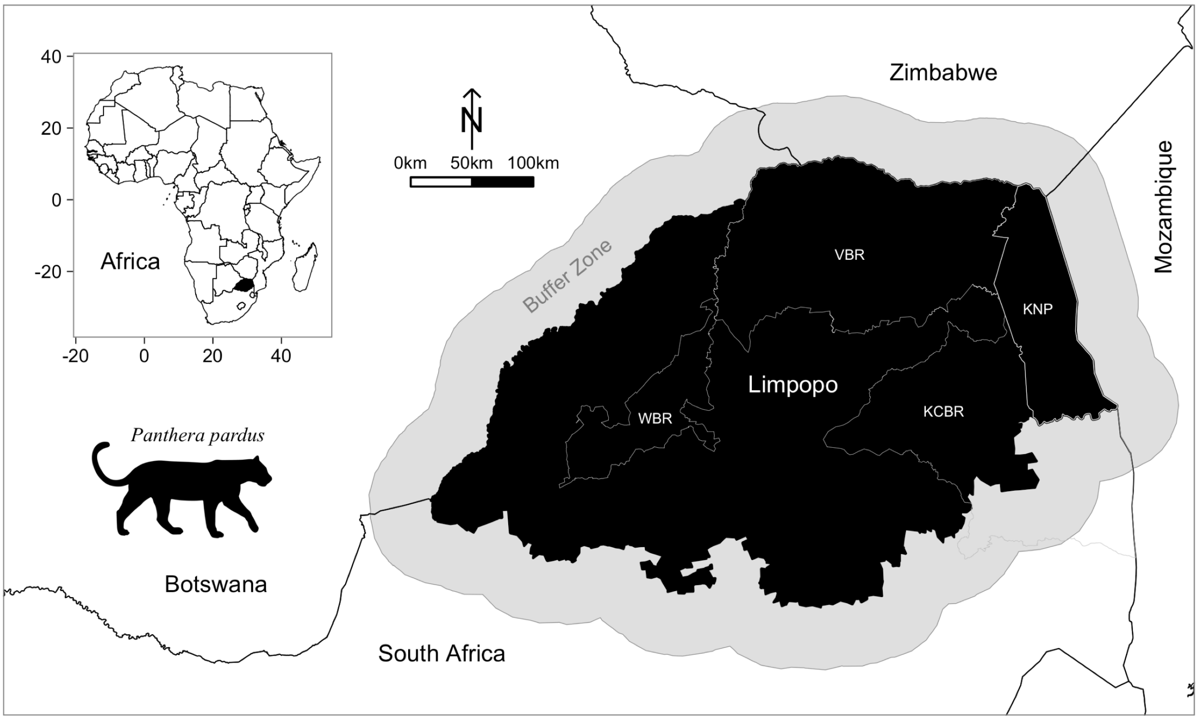


Figure 4.1. Location of the study area situated between northern South Africa, Botswana, Zimbabwe, and Mozambique. The grey region around Limpopo Province, South Africa ('Limpopo'; black polygon) represents the 50 km buffer used to develop an unbiased landscape permeability map. Limpopo represents a highly biodiverse region of southern Africa, comprising three UNESCO Biosphere Reserves: Waterberg Biosphere Reserve (WBR), Vhembe Biosphere Reserve (VBR), and Kruger to Canyons Biosphere Reserve (KCBR). Kruger National Park (KNP) lies adjacent to Limpopo's eastern boundary. Inset represents the location of the study area within Africa.

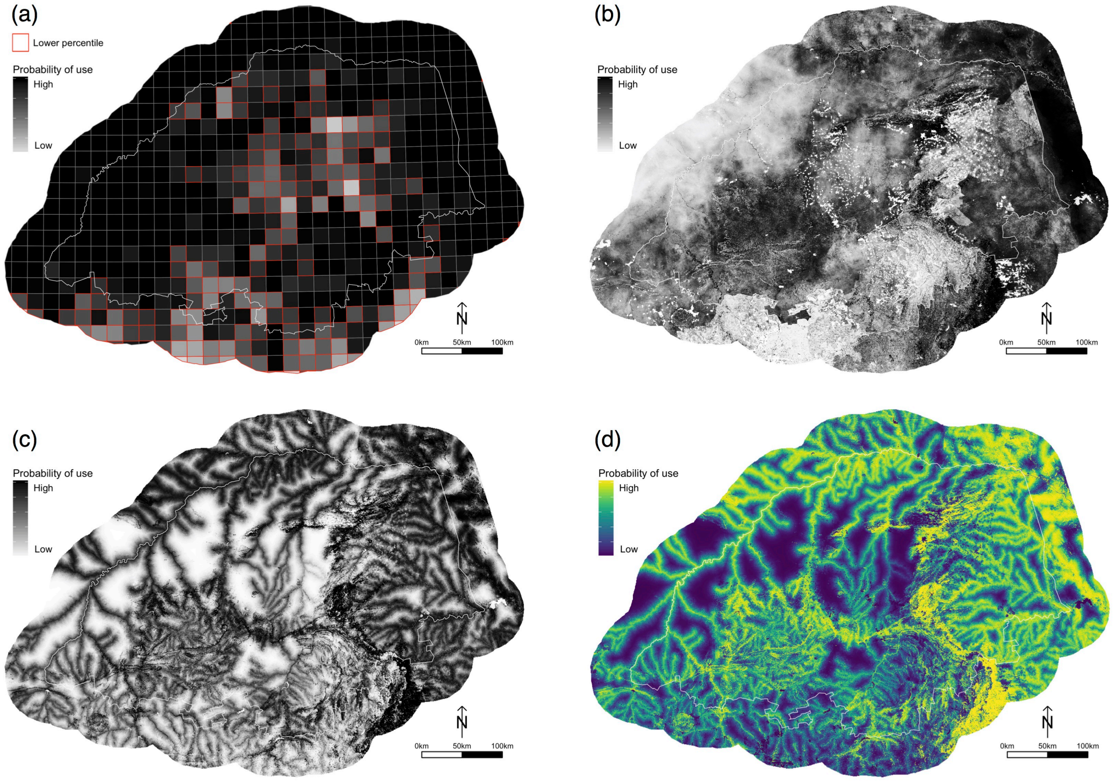


Figure 4.2. (a) Predictive map ($\psi$) depicting leopard *Panthera pardus* habitat use across the study area. Sampling cells outlined in red represent those that were omitted from the $S_2$ analysis (i.e., <25th percentile). (b) RSF map at $S_2$ scale of selection. (c) RSF map at $S_3$ scale of selection. (d) Scale-integrated resource selection function (SRSF). White overlay represents the administrative boundary of Limpopo Province, South Africa. Units represent values from low (0) to high (1).

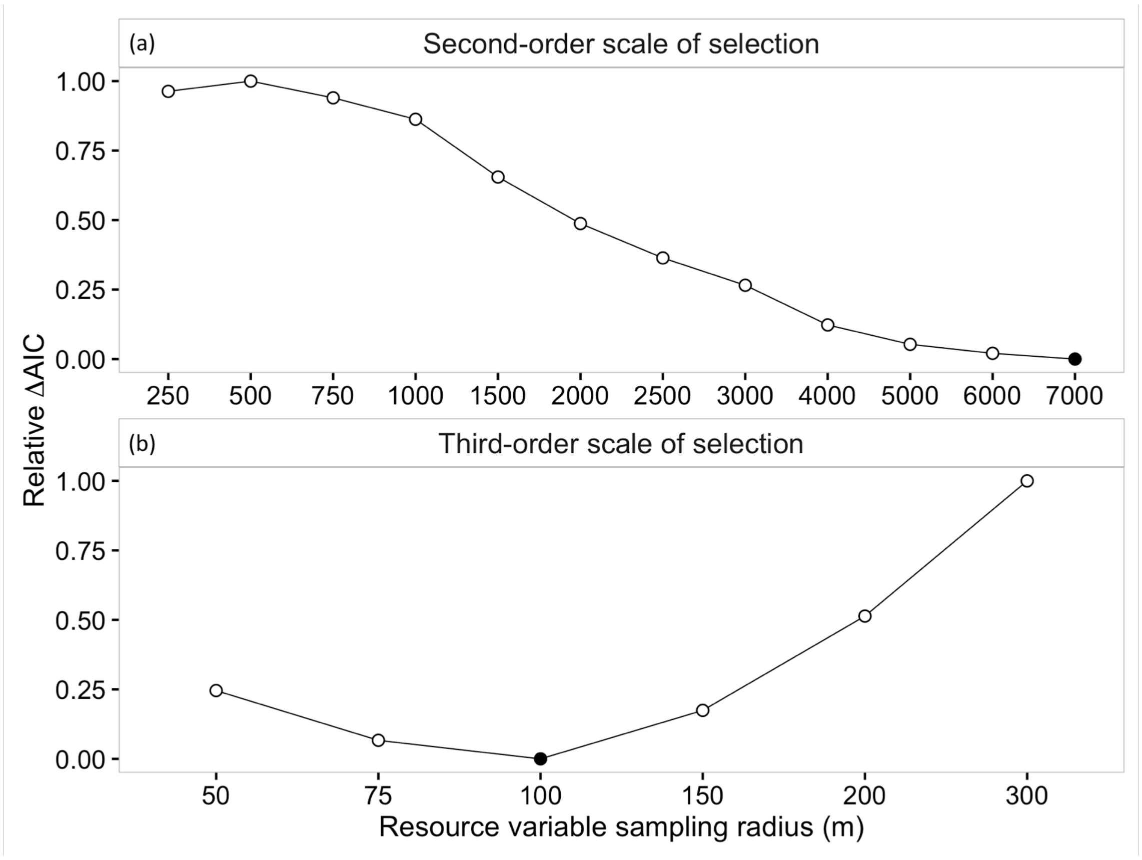


Figure 4.3. Relative ΔAIC ($\Delta AIC/\Delta AIC_{max}$) of (a) fixed- and (b) mixed-effect logistic regression models for $S_2$ and $S_3$ scales of selection, respectively. Black points represent optimum resource variable sampling radii.

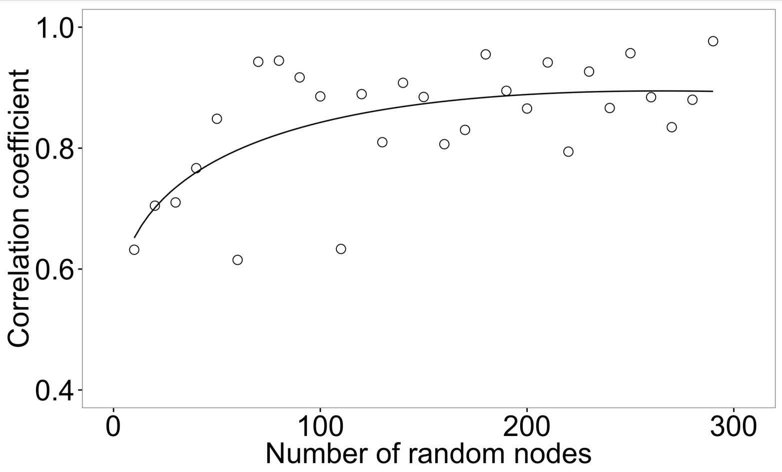


Figure 4.4. Pearson correlation coefficients of extracted values (n = 100,000) from a full permeability map developed using 300 random nodes compared to extracted values from permeability maps developed using fewer random nodes (i.e., 10–290).

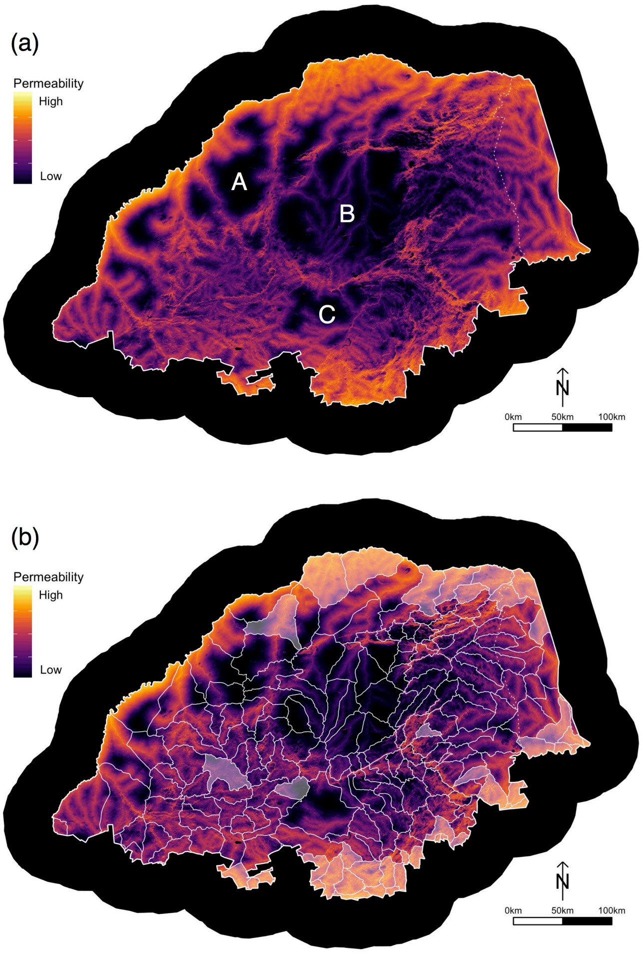


Figure 4.5. (a) Full permeability map developed using 300 regularly distanced random nodes around the buffer periphery. Three key regions (A, B and C) are characterized by markedly low habitat permeability. Clear habitat linkages are visible between regions A–B and B–C, which likely require focussed conservation effort. (b) Full permeability map overlaid with above- (opaque polygons) and below-optimal (transparent polygons) leopard management units (LMUs). The SRSF, used to develop the permeability maps, was resampled to 500m x 500m for computational efficiency. Units represent values from low (0) to high (1). Kruger National Park is depicted by the dotted polygon.

# CHAPTER 5 – Sustainable hunting: feasible or fallacy?

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## 5.1 ABSTRACT

Effective management of terrestrial hunting systems requires robust data to guide sound management practices. Obtaining quality demographic data, however, remains a challenge and often results in ad hoc hunting policies and potentially unsustainable hunting practices. In addition, illegal killing and state-sanctioned lethal control of putative problem animals represent additive forms of mortality, which are often not recorded. Here we examined how leopards *Panthera pardus* respond to different levels of hunting pressure, whilst considering multiple forms of anthropogenic mortality, to identify hunting scenarios that result in stable or increasing population growth.

Hunting always resulted in some degree of population decline. Hunting of successively older male leopards led to improved demographic projections, yet no realistic hunting scenario yielded stable or increasing population growth rates. Furthermore, the inclusion of female cohorts ≥7 years had a significant impact on population persistence. When accounting for minimum aging error (9%), a ≥7 year hunting restriction on male leopards resulted in population declines. When considering a low rate of additional mortality (1%; illegal killing or problem animal control) under a ≥7 year hunting scenario, leopard populations declined, even as harvest rates were reduced from 100% to 10%. Implementing two- or three-year recovery periods (i.e., intermittent moratoria on hunting) alleviated population declines, but failed to allow sufficient population recovery to ensure stable or increasing population growth rates. Population growth rates stabilized only once all forms of additive mortality were removed, together with a 40% harvest rate of males ≥7 years, and a minimum degree of aging error.

A combination of hunting regulations should be used to mitigate leopard population declines where a multifaceted and adaptive approach is adopted and additional forms of

mortality are significantly reduced (to <1% of the total population). Although we investigated hunting scenarios for leopards, the challenges faced by leopard management and conservation are equally present in other terrestrial hunting systems for which this approach is either directly applicable, or contributes theoretically.

## 5.2 INTRODUCTION

On a global scale, populations of terrestrial large mammals have markedly declined (Estes *et al.* 2011; Ripple *et al.* 2014). Recent research has begun to reveal the extensive cascading effects of these declines across ecosystems worldwide (Estes *et al.* 2011). One the many factors responsible for these global declines is recreational hunting (Caro *et al.* 2009; Creel *et al.* 2015); a form of additive mortality that remains a relatively easy practice to regulate and is often used for management purposes (Creel *et al.* 2015). Recreational hunting of wild animals is posited to provide considerable conservation benefits, from fostering tolerance of wildlife to securing their habitat (Lindsey *et al.* 2006). However, data required to effectively manage hunting is often lacking (Edwards *et al.* 2014). To counter these data deficiencies, conservation authorities are required to monitor wildlife populations at scales that are meaningful to management (Delsink *et al.* 2013). The stochastic nature of environmental and demographic processes, together with our limited understanding of how species respond to hunting, often render monitoring data unreliable or characterised by high uncertainties (Hauser, Pople & Possingham 2006; Nuno, Milner-Gulland & Bunnefeld 2014). Given these uncertainties, data deficiencies around wildlife monitoring and management remain a major challenge for management authorities and often lead to unsustainable (i.e., defined here as a unstable or declining population, or a population operating in a depressed, stable state) hunting practices (Caro *et al.* 2009; Nuno, Milner-Gulland & Bunnefeld 2014; Pitman *et al.* 2015).

The motivation for recreational hunting ranges from revenue generation to species persistence (Caro et al. 2009). Although not necessarily conflicting, such diverse drivers may result in a lack of consensus, and increased distrust and non-compliance, between the resource user and the establishment responsible for regulating hunting practices (Bunnefeld *et al.* 2013). In addition to recreational hunting, illegal killing and state-sanctioned lethal control of putative problem animals represent additive forms of mortality (Pitman *et al.*

2015), which impose even greater human-mediated pressure on wildlife populations (Robinson *et al.* 2014). Given the global decline of biodiversity and the economic fragility of many developing nations (Brooks *et al.* 2006; Allen & Giovannetti 2010), there exists an urgent need to develop robust methods for managing hunting in ways that optimise species conservation and wildlife-based revenue generation (Creel *et al.* 2016), but which account for additional forms of species mortality.

The removal of important demographic classes (e.g., primary breeders or territorial males) can detrimentally impact population persistence, and ultimately compromise the sustainability of hunting (Milner, Nilsen & Andreassen 2007; Packer *et al.* 2009; 2011). This is particularly evident for large carnivores (Caro *et al.* 2009)—a guild that garners considerable interest among hunters and conservationists alike. Given their important role in reproduction and recruitment, the hunting of female large carnivores is generally prohibited. However, population persistence can equally be threatened when males are hunted, since their removal can artificially trigger infanticide (i.e., the killing of conspecific young) by disrupting social cohesion through compensatory immigration (see Balme & Hunter 2013). For polygamous large carnivores, infanticide likely represents an adaptive behaviour that provides considerable reproductive benefits to perpetrators by shortening interbirth intervals of mothers, thereby increasing the likelihood of perpetrators siring subsequent litters (Whitman *et al.* 2004; Bellemain *et al.* 2006; Balme & Hunter 2013). Age-restricted harvesting has been advocated as one way to reduce the cascading impacts of infanticide on hunted populations, as it allows males sufficient time to sire at least one cohort of young to independence (Whitman *et al.* 2004; Packer *et al.* 2009; Balme, Hunter & Braczkowski 2012).

African lions *Panthera leo* and cougars *Puma concolor* frequently dominate demographic studies on large felids (Lambert *et al.* 2006; Whitman *et al.* 2007; Cooley *et al.* 2009; Packer *et al.* 2009; 2013; Edwards *et al.* 2014; Palmer, Fukuyama & Relman 2015), whereas less emphasis is afforded to other large felids occupying similar ecological niches, but which are exposed to equivalent, and sometimes greater, hunting pressures (Balme *et al.* 2010; Swanepoel *et al.* 2014a; Pitman *et al.* 2015; 2016). Here we simulate leopard *Panthera pardus* demographic responses to different levels of hunting pressure by parameterising an age- and sex-structured, stochastic matrix model using an extensive demographic dataset (Balme *et al.* 2012). We then apply the model across the broader landscape to explore the effects of hunting policy at a scale relevant to leopard management at a national scale.

Leopards are a highly sought after trophy animal that yield important ecological and economic benefits (Lindsey, Roulet & Romanach 2007; Dalerum *et al.* 2008), yet long-term population data are either locally-specific, unreliable or completely absent (Balme *et al.* 2014). Leopards are also frequently implicated in conflict situations (most of which goes unreported; see St John *et al.* 2012), due to the threat that they pose to livestock and people (Pitman *et al.* 2015). Accordingly, regulation of leopard hunting is characterised by informed guesswork, which often ignores additional forms of mortality, and leads to unsustainable hunting quotas (Balme *et al.* 2010; Pitman *et al.* 2015). Simulations studies have attempted to address aspects of hunting, and their effect on leopard populations (Caro *et al.* 2009; Swanepoel *et al.* 2014a), yet neither study incorporated the age-sex variation in hunting scenarios, age-sex specific additive mortality, the mechanistic effect of infanticide, and the inclusion of age-based error, nor the addition of hunting moratoria within one holistic approach. In particular, the practical application of an age minimum threshold for harvested male leopards has recently been evaluated (Balme, Hunter & Braczkowski 2012), following recommendations from a simulation study (Packer *et al.* 2009). These simulations, however, were parameterised using limited demographic data, and did not account for additional stochastic forms of mortality. Questions therefore remain over which leopard hunting scenarios result in a stable or increasing population.

In this study, we use over forty years of leopard demographic data from the Sabi Sand Game Reserve (SSGR), South Africa, to simulate how leopards respond to a range of hunting scenarios implemented at a national scale. SSGR represents a leopard population regulated by natural factors (Balme *et al.* 2012). Population dynamics within SSGR likely represent an 'ideal' situation in which to examine the effects of hunting devoid of confounding human-mediated pressures and enables the examination of hunting scenarios applied to a theoretical population (i.e., assuming the South African leopard population represented a best case scenario where human-mediated mortality was entirely absent). We modelled the long-term impacts of various hunting scenarios separately and in combination, comprising: (a) no hunting; (b) male and female harvest; (c) male-only harvest; (d) age-restricted male harvest with and without aging uncertainty following aging error rates described by Balme et al (2012); (e) addition of recovery periods (i.e., hunting followed by non-hunting periods to allow population recovery) (Creel *et al.* 2016); and, finally, (f) the addition of illegal killing and/or state-sanctioned lethal control of leopards as a stochastic additive process. Although we investigated the sustainability of various hunting scenarios for leopards, the challenges faced by leopard management and conservation are equally present in other terrestrial hunting systems—particularly large- and medium-sized felids—for which this approach is either directly applicable or contributes theoretically.

## 5.3 METHODOLOGY

### 5.3.1 Dynamic operating model

We modelled leopard population dynamics using an age- and sex-structured, stochastic matrix model

$$N_{t+1} = M_t(N_t - k_t),$$

where $N_t$ is the population size at time $t$, $k_t$ a vector of numbers killed at time $t$, and $M_t = B_n A S_t$ whose model components are described below. Demographic rates used in the model were based on long-term research (Balme & Hunter 2013) comprising 14 age-sex classes (Table 1). Demographic data from SSGR included complete life histories of 480 individuals (108 females, 114 males, and 258 cubs and juveniles) monitored from 1975 to 2015. Demographic stochasticity was introduced by making the parameters in matrix $M$ probabilities of transition, such that actual numbers were sampled from Poisson and Binomial distributions with probabilities corresponding to the transition matrix following Edwards et al. (2014) (see Table 1 for parameter values, with standard error provided in parentheses).

### 5.3.2 Survival, $\boldsymbol{S_t}$.

Using demographic data from previous research on SSGR (Balme *et al.* 2012), we derived estimates of survival using the Kaplan-Meier method (Pollock, Winterstein & Conroy 1989) calculated using the R package *survival* (Therneau 2016). We right censored individuals that disappeared, or were still alive, at the end of each year. This gives us our empirical survivorship estimates listed in Table 1. Cub and juvenile survivorship estimates include two important processes that change dynamically, and which need to be incorporated in the model structure. The first of these is infanticide, and the second, is a maternal effect (i.e., younger females typically have more resilient offspring) (Balme *et al.* 2012).

We included infanticide, which is likely to increase as a result of hunting (Balme & Hunter 2013), by making cub survivorship dependent on resident adult male survival. To determine whether there is a male present to mate with a female should a resident male die, we describe the probability of encounter per harem (defined as the number of females a male successfully sires cubs with in a single year), between males and harems using the harmonic mean:

$$\pi^{[E]} = \frac{2n_m n_h}{n_m + n_h}\frac{1}{n_h} = \frac{2n_m}{n_m + n_h}$$

where $n_m$ and $n_h$ refer to the number of males and harems, respectively, after mortality has been applied to the current time step. The probability of infanticide $\pi^{[I]}$ is then given as

$$\pi^{[I]} = \pi^{[E]}\left(1 - s^{[M]}\right)$$

where $\left(1 - s^{[M]}\right)$ is the probability of a resident male dying. The relationship between infanticide probability and adult male survivorship is therefore linear for a constant number of males (Creel *et al.* 2016), but highly non-linear when male mortality is taken into account. At intermediate levels of male mortality, infanticide is at its highest, but as mortality increases there are fewer males and infanticide starts to decline.

In summary, cub survivorship, adjusted for infanticide, can be written as

$$s_1 = \tilde{s}_1\left(1 - \pi^{[E]}\left(1 - s^{[M]}\right)\right)$$

where $\tilde{s}_1$ represents cub survivorship in the absence of infanticide (i.e., a baseline survival rate). Estimating $\tilde{s}_1$ takes place when the model is initialised, so that $s_1$ equals the current empirical value (supplied as a model input; Table 1).

Empirical data indicate that younger females are more successful at rearing cubs (Balme *et al.* 2012). To incorporate the effect of maternal age on both cub and juvenile survivorship we track the numbers born to each maternal age category within the model and then calculate a weighted average survival for cubs and juveniles at each time step. Our approach therefore derives a function for cub survival that accounts for infanticide, which in turn is a function of the sex ratio and male survivorship, and a maternal age effect on survivorship for both cubs and juveniles. Following a stochastic process, realised survival rates are updated at each annual time step, resulting in a time dependent survival matrix

$$S_t = \begin{bmatrix} s_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_6 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & s_7 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_8 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_9 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{10} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{11} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{12} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{13} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{14} \end{bmatrix},$$

with input survival rates given in Table 1.

To account for environmental fluctuations, the model included correlated variation in vital rates by sampling from a truncated log-normal distribution with a coefficient of variation ($cv$) of 20% (Edwards *et al.* 2014).

### 5.3.3 Births, $\boldsymbol{B_n}$.

Average age of first parturition for female leopards is 46 months (Balme *et al.* 2012); hence, in the model, only adult females were reproductively active. Although male leopards are capable of mating from three years old, average age of first reproduction is five years (4.96 ± 0.20 SE, range = 3–7 years, n = 19; G. A Balme unpublished data); therefore, within the model, only males >60 months were considered reproductively active. The number of births is the product of the number of mating opportunities and the number of cubs produced by each opportunity. The number of mating opportunities is the harmonic mean (i.e., $\frac{2n_m n_h}{n_m+n_h}$) of the number of males ($n_m$) and the number of female harems ($n_h$; where $n_h = \frac{n_f}{h}$ where $n_f$ is the number of females and $h$ is the harem size). If each female in a harem produces $C$ cubs, then the average number of cubs produced by a harem per mating opportunity is the total number of cubs ($n_f C$) over the total number of harems (i.e., $\frac{n_f C}{n_h} = Ch$). However, for leopards, survivorship of dependent young (i.e., cubs and juveniles) is directly related to the age of the mother (Table 1) (Balme *et al.* 2012), such that the number of cubs per harem is given as: $\sum \frac{n_{fa} C_a}{n_h}$, where subscript $a$ denotes mothers of different ages. The birth function is therefore given as

$$B(n_m, n_f, h, C) = \sum n_{fa} C_a . \frac{2n_m}{n_m + n_h}.$$

Hence, the birth function can be used to calculate the fecundity functions for males and different female age classes:

$$B(n_m, n_f, h, C) = n_m F_m + \sum n_{fa} F_{fa}$$

where $F_m$ and $F_{fa}$ are the respective fecundities per individual. Therefore, the fecundity functions for males and females are given as

$$F_m = \frac{\sum n_{fa} C_a}{n_m + n_h}$$
$$F_{fa} = \frac{n_m C_a}{n_m + n_h},$$

and the number of births in each female age category ($B_a$) can therefore be calculated as

$$B_a = \frac{2n_m n_{fa} C_a}{n_m + n_h},$$

giving the birth matrix

$$B_n = \begin{bmatrix} 0 & 0 & 0 & F_{fa} & F_{fa} & F_{fa} & F_{fa} & F_{fa} & 0 & 0 & 0 & F_m & F_m & F_m \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}.$$

### 5.3.4 Harem Size, $\boldsymbol{h}$.

A key parameter in both cub survival and the birth rate is the harem size ($h$), which itself is a function of the number of males and females breeding in the population. Since female leopards do not necessarily breed every year, the probability of a female breeding in any one year is generally less than one (on average). In the current scenario $h$ = 1.14 (as described by the empirical data from SSGR) and since $n_m . h < n_f$, we can deduce that the probability that an adult female breeds ($\pi^{[B]}$) is approximately 0.83 at the current state. However, this is likely to change as the sex ratio changes, and this in turn, will influence the average harem size, which becomes a dynamic function of the population state:

$$h = \frac{n_f}{n_m} \pi_p^{[B]}$$

If the number of males in the population equals zero, then the probability of a female breeding will be zero; and if the proportion of males increases, then the probability of a female breeding will tend towards one. Therefore, $\pi^{[B]}$ exhibits the following properties:

$$g(p) = 0 \text{ when } p = 0 \text{ and}$$
$$g(p) \to 1 \text{ as } p \to \infty$$

A suitable, parsimonious functional form that expresses the above properties can be given as

$$g(p) = \pi_p^{[B]} = 1 - exp(-\beta . p)$$

Since $\pi_p^{[B]}$ and p is known (i.e. provided as empirical data on input), we can estimate beta during initialisation of the model.

### 5.3.5 Aging, $\boldsymbol{A}$.

The age transition matrix included the proportion of females at age two ($p = 0.5$; i.e., juveniles entering the adult cohort class were equally split between males and females) (Balme *et al.* 2012) and was given by

$$A = \begin{bmatrix}
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1-p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1
\end{bmatrix}.$$

### 5.3.6 Implementation of hunting scenarios

Leopards were removed from the population following two processes; first, in accordance with a specific hunting scenario, and, second, following a stochastic process to simulate illegal killing and/or state-sanctioned lethal control of leopards. Sequential repetition of these separate or combined processes at each annual time step produced vector $k$.

### *Baseline hunting scenario*

The baseline hunting scenario (i.e., a scenario with no hunting) involved leaving the simulated leopard population to regulate itself without any form of anthropogenic mortality. Hunting scenarios were applied to specific age-sex classes based on the proportion of those age classes within the simulated population.

### *Age minimum restrictions for males and females*

Given that leopard population sizes are unknown—with the exception of relatively small and intensively monitored survey sites (Balme, Hunter & Slotow 2009)—we first evaluated hunting scenarios by simulating the removal of 100% of a particular age-sex class. Rationale for this approach stems from the challenge in prescribing a quota limit of <100% where true population size is largely unknown. We simulated the 100% removal of male leopards from ≥3 years through to ≥7 years. To better understand the effect of hunting female leopards within our simulated population, we assessed the removal of 100% of females ≥7 years.

It is impossible to reliably distinguish male (<7 years) or female (of any age) leopard age classes based on phenotypic traits (Balme et al. 2012). Therefore, we present simulations on a variety of age minimum thresholds (without incorporating any aging error; see below) for males <7 years and females ≥7 years for heuristic purposes; such scenarios could not be practically implemented in the field (Balme, Hunter & Braczkowski 2012). We included the hunting of females ≥7 years since calls to hunt adult female leopards remains high on regulatory agendas across the study area (R Pitman, *personal observation*).

### *Incorporating aging error*

Although survey methodologies have markedly improved (O'Connell, Nichols & Karanth 2011; Hamel *et al.* 2012; Royle *et al.* 2014), obtaining accurate population estimates across large spatial scales remains a pervasive issue—particularly for wide-ranging and elusive species such as large carnivores (Balme, Hunter & Slotow 2009). Age minimum restricted hunting scenarios therefore offer a potential advancement over historical quota setting approaches insofar as they enable potentially responsible hunting practices without the reliance on ad hoc population estimates (Balme, Hunter & Braczkowski 2012). Discriminant models developed by Balme et al. (2012) demonstrated that male leopards ≥7 years could be reliably distinguished on 91% of occasions, based on key phenotypic traits such as dewlap size, ear condition, and facial scarring. Accordingly, we applied an aging error of 9% in models assessing the impacts of an age-restricted harvest of male leopards ≥7 years.

### *Additive forms of mortality*

Although recreational hunting of large carnivores remains an additive form of mortality for hunted populations (Caro *et al.* 2009; Packer *et al.* 2009), illegal killing and indiscriminate problem animal control represent far greater risks to population persistence (Swanepoel *et al.* 2014a; Pitman *et al.* 2015; 2016). Illegal killing and/or state-sanctioned lethal control of leopards is typically non-target specific (Pitman *et al.* 2015; 2016). As such, males and females from all age classes were eligible for removal under these scenarios. Stochastic additive mortality was, therefore, applied by randomly removing a pre-defined proportion of leopards from the total number of leopards within all age classes.

### *Incorporating intermittent recovery periods*

Given the decline in growth rates from historical harvest scenarios (Caro *et al.* 2009; Packer *et al.* 2009), we incorporated recovery periods under a ≥7 year male-only hunting scenario to investigate how our simulated leopard population would respond to intermittent moratoriums on hunting (Creel *et al.* 2016). Two different recovery periods were used: two- (two years on, two years off), and three-year (three years on, three years off) recovery periods. These temporal scales were chosen since they should theoretically allow the simulated leopard population to recover from the immediate effects of hunting (i.e., sufficient time has passed for at least one litter to potentially reach independence; Balme et al. 2012b).

### *Reducing harvest rates below 100%*

Severe data deficiencies exist for leopard—and other carnivore—populations at broad geographic scales. As a result, conservation practitioners and policy makers are often required to adopt the precautionary principle; defined as a strategy to avoid or mitigate potential, and scientifically plausible risks to nature in situations where scientific certainty is absent (UNESCO 2005). In an attempt to identify a hunting scenario under the precautionary principle, conservation practitioners could reduce harvest rates by implementing a reduced hunting quota (i.e., <100% of the targeted age class). As a final assessment, we reduced harvest rates of male leopards ≥7 years below 100% (i.e., simulating a precautionary principle approach) to investigate the potential for leopard hunting to result in stable or increasing population dynamics whilst accounting for other limiting factors (e.g., aging error, illegal killing, and problem animal control). It is worth noting that prescribing a harvest rate of <100% remains challenging, if not impossible, since true population size is not known. Nevertheless, for heuristic purposes, we believe these assessments will benefit management authorities.

### 5.3.7 Model simulations

To maintain consistency across hunting scenarios, and to evaluate scenarios applicable to key hunting regions in southern Africa, our modelled population exhibited a starting demographic structure identical to SSGR, and a starting population size of 4,480 individuals to simulate hunting at a national scale (i.e., South Africa; see Swanepoel et al. 2014 for estimates of population size). Given the high degree of parameter variation (i.e., $cv$ of 20%) included within the model, and the model's ability to accommodate larger starting population sizes (Supporting Information S1), we believe our approach to extrapolate hunting scenarios at a national scale to be justified. Although leopard demographic parameters exist for other regions in Southern Africa (Swanepoel *et al.* 2014a; b), these data sets are unable to match the high data resolution required by our model, but which are provided by the SSGR data set.

The model was developed in R (R Core Team 2016) and implemented using package *leopard* (https://github.com/cttedwards/leopard). Density dependent population dynamics were excluded from the model since data required to inform this process were largely absent. Each hunting scenario simulation was run for 50 years (following initialisation of the model; *n* = 10 time steps) with 1000 Monte Carlo replicates, from which we report population size, average growth rate (lambda; $\lambda$), and numbers harvested.

## 5.4 RESULTS

The baseline hunting scenario (Fig. 5.1a) resulted in stable stochastic demographic rates with $\lambda$ at 1.01 (population increase of 1% year$^{-1}$). Although some hunting scenarios caused fewer detrimental effects on population viability than others, all realistic hunting scenarios always resulted in some degree of population decline.

### 5.4.1 Age minimum restrictions for males and females

Recreational hunting of successively older male leopards led to improved demographic projections (from $\lambda_{3yrs} = 0.79$ to $\lambda_{7yrs} = 1$; Fig. 5.1b–e). Our results demonstrated that the inclusion of male and female cohorts ≥7 years had a negative impact on population persistence, with $\lambda$ at 0.81 (population decline of 19% year$^{-1}$; Fig. 5.2). Importantly, these simulated declines did not account for aging error by hunters, which is highly evident for male leopards (Balme, Hunter & Braczkowski 2012), and likely more so for female leopards since they lack the characteristic phenotypic traits (e.g., large head, muscular body, and prominent dewlap) used the distinguish ≥7 year male leopards from other male and female cohorts (Balme, Hunter & Braczkowski 2012).

### 5.4.2 Incorporating aging error

With the removal of 100% of males ≥7 years, and the implementation of a 9% error rate in aging, our model yielded a $\lambda$ of 0.99 (population decline of 1% year$^{-1}$; Fig. 5.3). This scenario assumed that no additional human-mediated forms of mortality are imposed on the population, which remains an unrealistic depiction of leopard populations across southern Africa, and further afield (Jacobson *et al.* 2016).

### 5.4.3 Additive forms of mortality

As our results demonstrated, when we considered a reduced rate of additional mortality (i.e., 1% illegal killing or problem animal control) under a ≥7 year male-only hunting scenario (Fig. 5.4), the population continued to decline, with $\lambda$ at 0.97 (population decline of 3% year$^{-1}$). These findings are largely due to the indiscriminate removal of key demographic classes (Caro *et al.* 2009), such as females and dependent young, which even at this conservative rate of additive mortality, caused enough disturbance to destabilise our simulated population.

### 5.4.4 Incorporating intermittent recovery periods

Consistent with expectations, implementing two- or three-year recovery periods alleviated the immediate impact of hunting, but consistently failed to allow sufficient population recovery (Fig. 5.5a–b); for two- and three-year scenarios, our simulations yielded $\lambda$ at 0.99 (population decline of 1% year$^{-1}$) and 0.99 (population decline of 1% year$^{-1}$), respectively.

### 5.4.5 Reducing harvest rates below 100%

Our results demonstrated that even when additive forms of mortality are held at reduced levels (i.e., illegal killing and problem animal control at 1%), population projections continued to decline even as harvest rates of males ≥7 years are reduced to 10% (Fig. 5.6a–c). Only once all forms of additive mortality are removed, together with the implementation of a 40% harvest rate with a minimum level of aging error (9%), did we identify a potentially sustainable hunting scenario with $\lambda = 1$ (Fig. 5.6d). This harvest scenario would theoretically permit the removal of 82 ± 0.003 SE male leopards ≥ 7 years each year (Fig. 5.7), but assumes no additional human-mediated mortality occurs.

## 5.5 DISCUSSION

Leopards are sensitive to human-mediated mortality, as demonstrated in this study and others (Caro *et al.* 2009; Packer *et al.* 2009; 2011). Although recreational hunting of leopards often resulted in some degree of population decline, our findings are consistent with earlier research, which demonstrated that age minimum harvest strategies of male cohorts can potentially lead to more sustainable hunting practices (Whitman *et al.* 2004; 2007). For recreational hunting of males ≥7 years, our findings are also consistent with later research, which suggested that restricting hunting to male leopards ≥7 years would ensure sustainability, regardless of the extent of offtake (Packer *et al.* 2009; Balme, Hunter & Braczkowski 2012). However, when accounting for minimum aging error (9%) under a ≥7 year male-only hunting scenario, population projections began to decline. This minimum level of aging error assumes recreational hunters are highly accurate at distinguishing the ≥7 year male leopard age class. However, this remains unlikely given the conditions in which leopards are baited and shot from a hide (Balme, Hunter & Braczkowski 2012). Hunting expeditions are typically carried out at night, when visibility is poor, and therefore, aging accuracy is unlikely to be high (Balme, Hunter & Braczkowski 2012). Such implications could result in an aging error rate >9%, which would have further detrimental implications for leopard population persistence.

Across most African range states, the hunting of female leopards is prohibited (Lindsey *et al.* 2013b). This approach appears sensible, and prudent, given that the inclusion of female cohorts ≥7 years within our simulations had negative implications for population persistence. Female leopards represent primary breeders that are largely philopatric, and typically produce two cubs per breeding event (Balme *et al.* 2012). As with other carnivores (Logan & Sweanor 2001; Goodrich *et al.* 2010), leopards form matrilineal assemblages (Balme *et al.* 2012)—females often relinquish parts of their territory to establishing daughters (Fattebert *et al.* 2015)—and suggests that females represent a fundamental component of leopard population structure (Balme *et al.* 2012). Consistent with our findings, the hunting of female leopards can result in declining reproductive success and increased social-spatial instability, which may ultimately drive overall population declines (Caro *et al.* 2009).

When considering a reduced rate of additional mortality (1%) under a ≥7 year male-only hunting scenario, leopard populations declined, even as harvest rates for this cohort were reduced from 100% to 10%. Although previous research has indicated that age minimum thresholds (i.e., hunting of all males ≥7 years) could theoretically remove 100% of a particular demographic class (Packer *et al.* 2009; Balme, Hunter & Braczkowski 2012), the decline in our simulated population is largely a result of aging error and the impact of infanticide on model projections. In addition, the illegal killing of leopards in southern Africa remains a pervasive issue where as many as 19% of farmers illegally kill at least one leopard every year (St John *et al.* 2012). The use of poison remains a popular method of destruction, with 21% of farmers using this adopting this method to kill carnivores; whilst 22% of farmers kill protected carnivore species (e.g., leopards) without valid permits (St John *et al.* 2012). This high degree of illegal behaviour strongly suggests that a reduced rate of additional mortality, as we demonstrate in this study, represents a potential gross underestimate of actual illegal activity.

Implementing two- or three-year recovery periods alleviated projected population declines, but failed to allow sufficient population recovery. When all forms of additive mortality were removed, together with a 100% harvest rate of male leopards ≥7 years, and a minimum degree of aging error, both hunting scenarios resulted in population declines. Nevertheless, this approach highlights the biological benefits, and population-level effects, of implementing moratoriums as a management strategy to alleviate human-mediated pressure on carnivore populations (Creel *et al.* 2016).

Leopards, and large carnivores more generally, are experiencing marked population declines across the world's ecosystems (Ripple *et al.* 2014; Jacobson *et al.* 2016). Although in theory, hunting may foster tolerance towards large carnivores (but see Chapron & Treves 2016; Teichman, Cristescu & Darimont 2016 for evidence that refutes this supposition), and may potentially generate funds necessary for their conservation (Lindsey *et al.* 2006), we highlight the many challenges associated with sustainable hunting practices. Recent research has shown that renewed policy changes are required for the recreational hunting of lions (Creel *et al.* 2016); a large carnivore with similar ecological and demographic characteristics to leopards (Caro & Stoner 2003; Caro *et al.* 2009). Any policy decisions for leopard management, however, need to be enforceable by authorities operating limited budgets. This simple fact has led to the perception that quota setting restrictions for leopards are not necessary, and that hunting practices could be solely based on unrestrictive age minimum criteria (i.e., removal of all males ≥7 years; Packer et al. 2009). This approach is largely enforceable through simple assessments of post-mortem trophy specimens (Balme, Hunter & Braczkowski 2012), which has led to its widespread adoption in carnivore management policies across Africa (Whitman *et al.* 2004; 2007; Packer *et al.* 2009; Balme *et al.* 2010; Lindsey *et al.* 2013b). However, our findings do not support an unrestrictive age minimum approach, but rather demonstrate that population declines occur when even 10% (with 9% aging error) of ≥7 year males are harvested. Given that leopard population sizes are largely unknown, deciding on a plausible sustainable quota limit will be challenging, and will most likely require adoption of the precautionary principle (UNESCO 2005) until more advanced scientific methods can be incorporated within the quota-setting process; such as the adoption of a management strategy evaluation framework (Bunnefeld, Hoshino & Milner-Gulland 2011; Bunnefeld *et al.* 2013; Edwards *et al.* 2014).

Our findings have significant implications for management insofar as isolated hunting regulations (e.g., age minimum approaches, or male-only harvest strategies) on their own will likely not be sufficient to mitigate leopard population declines. As we demonstrate, age minimum approaches, together with a male-only harvest, limited quotas, and zero additive mortality remain the only recreational hunting scenario capable of ensuring a stable or growing leopard population. These scenarios, however, require the unrealistic assumption that additive forms of mortality are largely absent and that hunters are highly proficient at identifying male leopards ≥7 years. Recreational hunting has long been regarded as a primary cause of population decline for large carnivores (Caro *et al.* 2009), yet, as we demonstrate, additive forms of mortality (e.g., illegal killing and problem animal control) remain far greater contributors to population declines and subsequent unsustainable management practices—particularly for large felids such as leopards (Caro *et al.* 2009; Pitman *et al.* 2015). Ultimately, additional forms of mortality need to be reduced (to <1% of the total population) before consumptive practices could be considered sustainable. These findings provide stakeholders (e.g., hunters, landowners, and governments) who wish to generate profits from recreational hunting clear incentives to assist in mitigating the illegal killing and indiscriminate problem animal control of leopards and other hunted species exposed to similar anthropogenic pressures (Bunnefeld *et al.* 2013).

Our findings are consistent with Creel et al. (2016), who suggest that increasing human pressures across Africa are likely to increase anthropogenic impacts on species survival (such as illegal killing), and thereby exacerbate population declines of large carnivores beyond the status quo. Given the current state of legal and illegal activities within African range states (St John *et al.* 2012), together with the limited capacity of government authorities to deal with increasing management pressures, our findings highlight the significant challenges faced by management authorities in prescribing sustainable hunting practices for leopards.

## 5.6 ACKNOWLEDGEMENTS

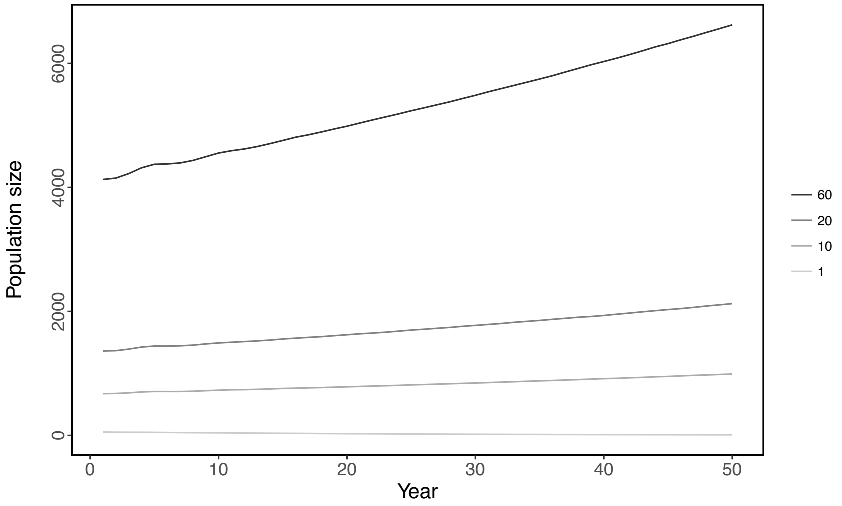
This research was funded by Panthera. RTP was supported by a South African National Research Foundation bursary (# 83690) and a Panthera Kaplan Graduate Award.

## 5.7 SUPPORTING INFORMATION

Supporting Information S1.

Given that our primary objective was to inform leopard management at a landscape scale, we first evaluated the degree to which our simulated leopard population was robust to starting population sizes before conducting any hunting simulations. This was achieved by a sensitivity analysis, whereby starting population sizes from Sabi Sand Game Reserve (SSGR) were adjusted by a range of multipliers (i.e., 1, 10, 20, and 60) at the first time step. This approach enabled evaluation of whether the model could be reliably applied to population sizes larger than that of the SSGR, and therefore, provide insight into leopard management more broadly.

Figure S1. Sensitivity analysis assessing the use of different multipliers on starting population sizes. Demographic rates are based on a protected leopard population from the Sabi Sands Game Reserve in South Africa. Given each multiplier, the model follows a linear and stable trajectory. The increasing rate of growth at larger starting population sizes is indicative of more breeding individuals present within the population (i.e., demonstrating exponential growth).



## 5.8 TABLES AND FIGURES

Table 5.1. Cohort structure and vital rates (standard error represented in parentheses).

| Notation | Age category | Age (months) | Survival rate | Birth rate |
|---|---|---|---|---|
| $N_1$ | Cub | 0–12 | $S_1$ = 0.32 (0.07) | – |
| $N_2$ | Juvenile | 13–24 | $S_2$ = 0.72 (0.08) | – |
| $N_3$ | Subadult female | 25–36 | $S_3$ = 0.96 (0.10) | – |
| $N_4$ | Adult female | 37–48 | $S_4$ = 0.89 (0.12) | 1.86 (0.08) |
| $N_5$ | Adult female | 49–60 | $S_5$ = 0.97 (0.12) | 1.84 (0.07) |
| $N_6$ | Adult female | 61–72 | $S_6$ = 0.94 (0.13) | 1.86 (0.12) |
| $N_7$ | Adult female | 73–84 | $S_7$ = 0.92 (0.14) | 1.92 (0.18) |
| $N_8$ | Adult female | >84 | $S_8$ = 0.72 (0.21) | 1.85 (0.06) |
| $N_9$ | Subadult male | 25–36 | $S_9$ = 0.91 (0.11) | – |
| $N_{10}$ | Adult male | 37–48 | $S_{10}$ = 0.96 (0.12) | – |
| $N_{11}$ | Adult male | 49–60 | $S_{11}$ = 1.00 (0.12) | – |
| $N_{12}$ | Adult male | 61–72 | $S_{12}$ = 1.00 (0.12) | – |
| $N_{13}$ | Adult male | 73–84 | $S_{13}$ = 0.90 (0.16) | – |
| $N_{14}$ | Adult male | >84 | $S_{14}$ = 0.29 (0.85) | – |

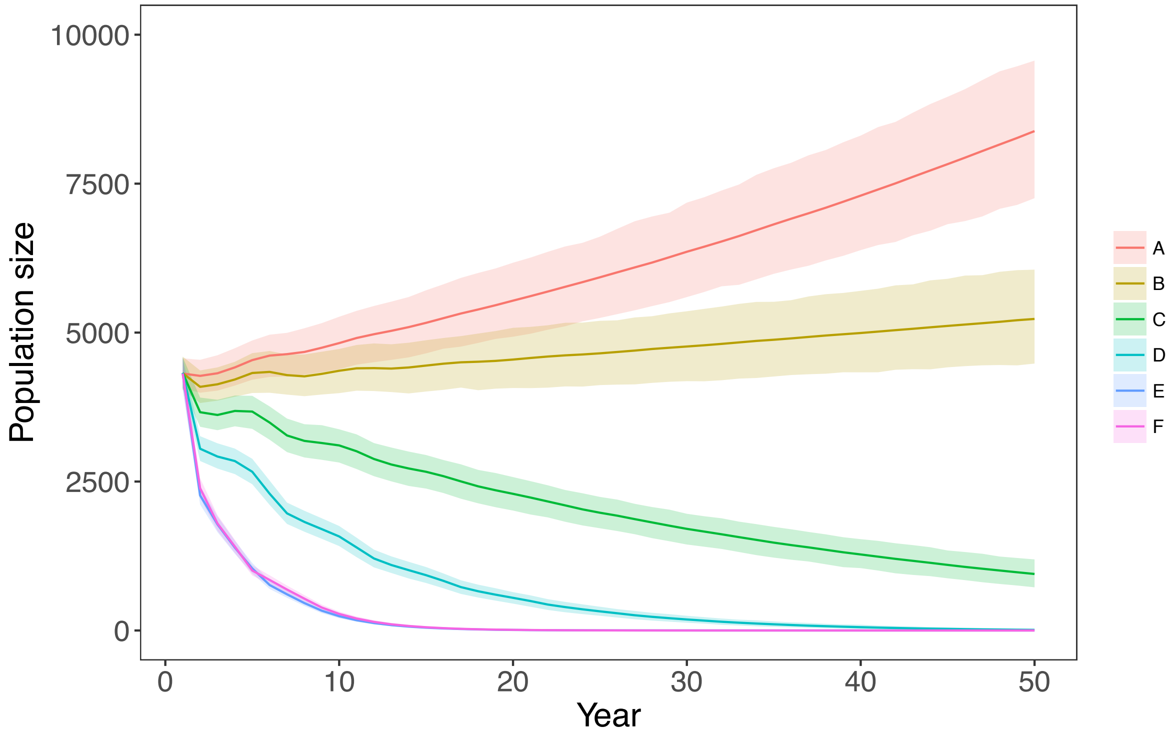


Figure 5.1. Projected mean population responses (shaded regions represent 95% CI) to 50 years (following an initialisation period; n = 10 time steps) of age minimum hunting restrictions for males. No hunting (a), hunting of all ≥7 years male cohorts (b), hunting of all ≥6 years male cohorts (c), hunting of all ≥5 years male cohorts (d), hunting of all ≥4 years male cohorts (e), hunting of all ≥3 years male cohorts (f).

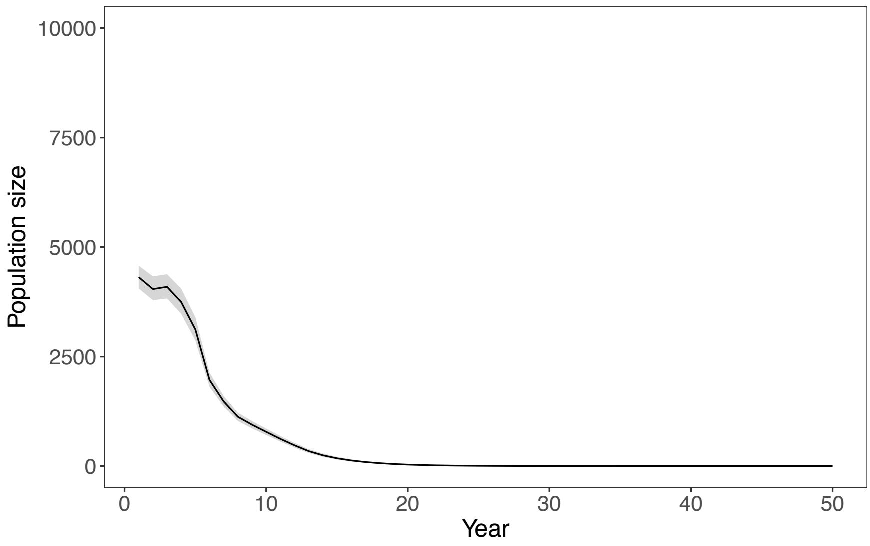


Figure 5.2. Projected mean population responses (shaded regions represent 95% CI) to 50 years (following an initialisation period; n = 10 time steps) of age minimum hunting restrictions (≥7 years old cohorts) for 100% of males and females.

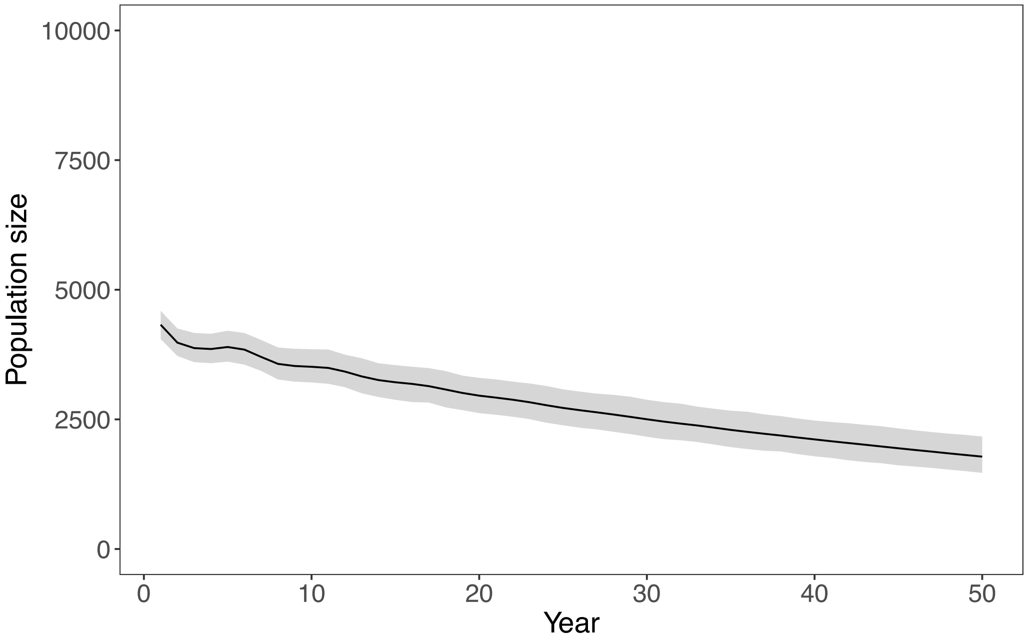


Figure 5.3. Projected mean population responses (shaded regions represent 95% CI) to 50 years (following an initialisation period; n = 10 time steps) of age minimum hunting restrictions for males with the inclusion of aging error. Aging error rate as described by Balme et al. (2012).

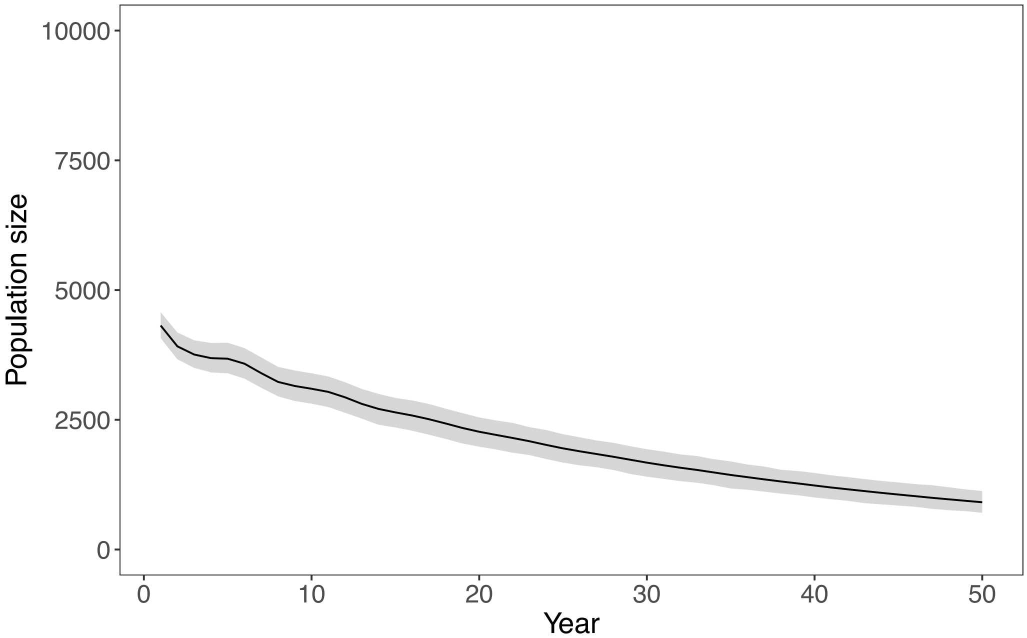


Figure 5.4. Projected mean population responses (shaded regions represent 95% CI) to 50 years (following an initialisation period; n = 10 time steps) of age minimum hunting restrictions for males with the inclusion of aging error and additional forms of mortality. Illegal killing or problem animal control at minimum levels. Both forms of mortality result in the same levels of population decline, as a result, we present only one graphical representation.

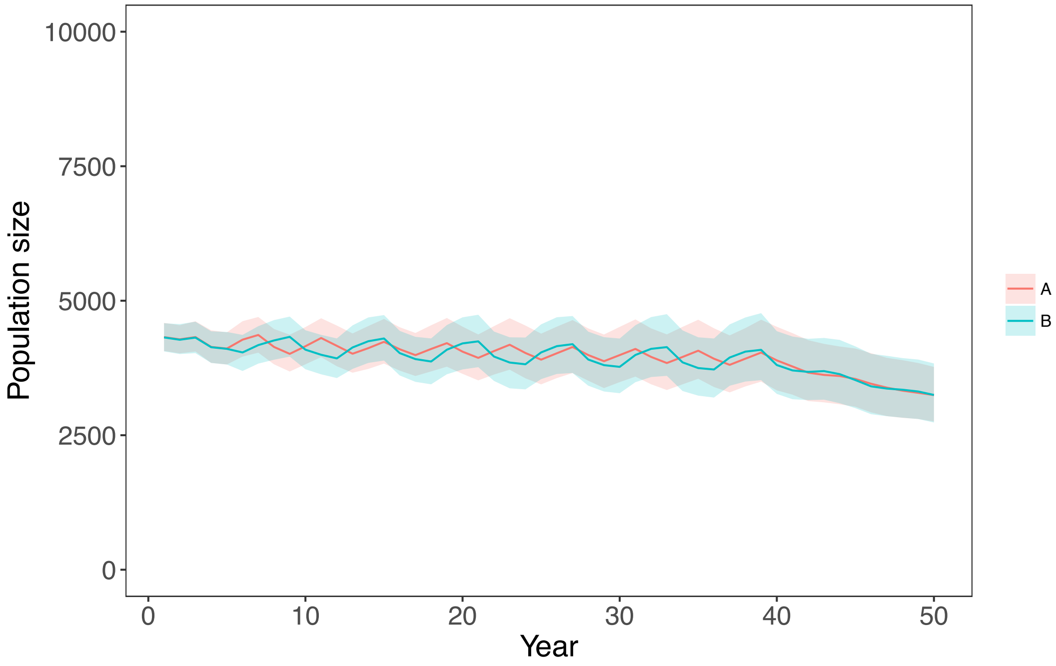


Figure 5.5. Projected mean population responses (shaded regions represent 95% CI) to 50 years (following an initialisation period; n = 10 time steps) of age minimum hunting restrictions for males with the inclusion of aging error and recovery periods. Two-year recovery periods comprising two-years of hunting followed by two-years of recovery (a), three-year recovery periods comprising three-years of hunting followed by three-years of recovery (b).

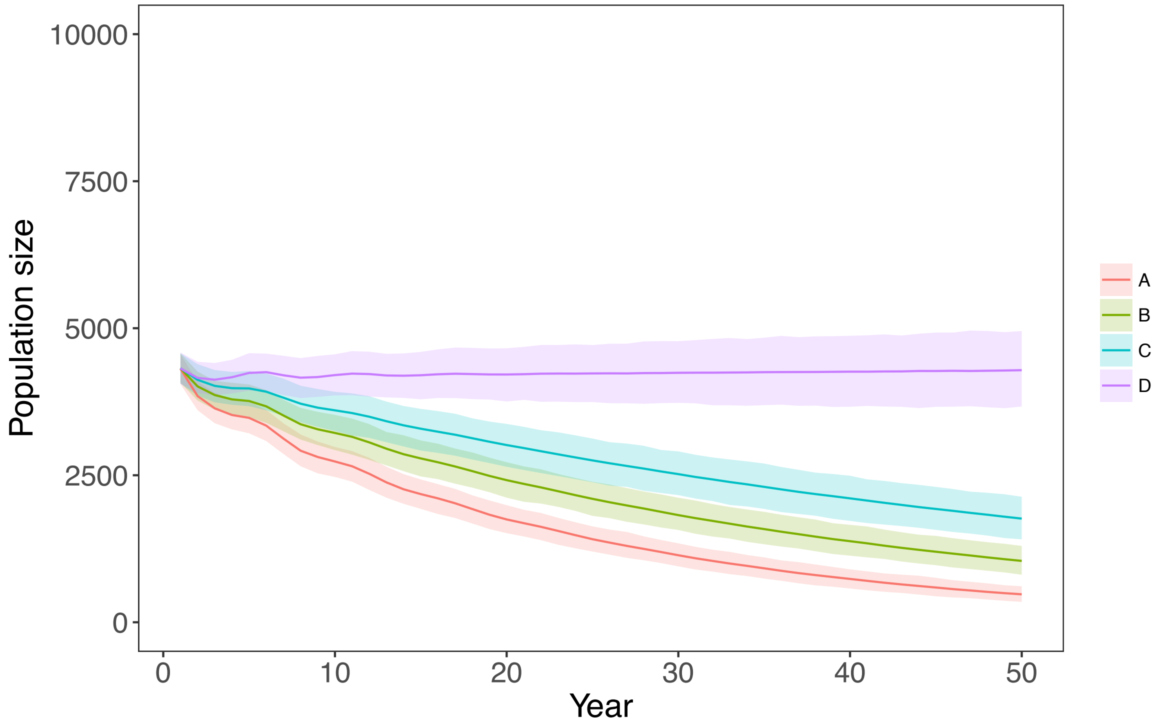


Figure 5.6. Projected mean population responses (shaded regions represent 95% CI) to 50 years (following an initialisation period; n = 10 time steps) of varying degrees of age minimum hunting restrictions for males with the inclusion of aging error and additional forms of mortality. Age minimum hunting restrictions applied to 100% of ≥7 year old males with minimum aging error (9%) (a), age minimum hunting restrictions applied to 50% of ≥ 7 year old males with minimum aging error (9%) (b), age minimum hunting restrictions applied to 10% of ≥ 7 year old males with minimum aging error (9%) (c), age minimum hunting restrictions applied to 40% of ≥ 7 year old males with minimum aging error (9%) and zero additional human-mediated mortality (*only potentially sustainable scenario*) (d).

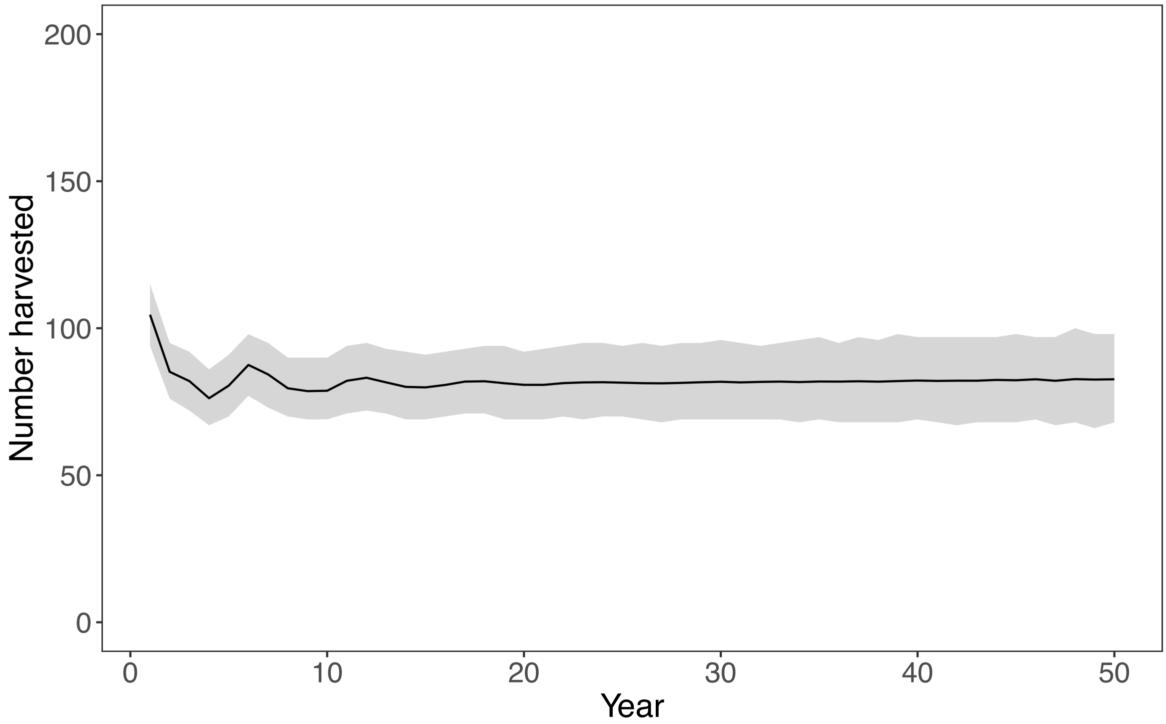


Figure 5.7. Average number of leopards harvested (shaded regions represent 95% CI) across 50 years (following an initialisation period; n = 10 time steps) of projected mean population responses to age minimum hunting restrictions applied to 40% of ≥ 7 year old males with minimum aging error (9%) and zero additional human-mediated mortality.

# CHAPTER 6 – Summary and conclusions

The purpose of this study was to assess fundamental components of wildlife management and conservation of large carnivores across a landscape dominated by people. In this chapter, I synthesize my findings and explore their broader applicability for large carnivore management and conservation in a data deficient world. Specifically, I will discuss the implications of my findings in the wider context of sustainable management, and how my work contributes to the field of management and conservation of large carnivores more widely. Although the context is provided using leopard management in northern South Africa, my findings exemplify the challenges associated with sustainable management of terrestrial hunting systems and large carnivore conservation more generally.

## 6.1 SCIENCE-BASED MANAGEMENT

Prioritizing areas of conservation concern remains a vital component in combating species declines. Human-mediated mortality represents one such major threat, resulting in an increasing need for improved management. However, large-scale management decisions are seldom supported by science-based evidence (Sutherland *et al.* 2004). In Chapter 2, I evaluated the extent and spatial distribution of legal anthropogenic offtake of leopards to identify *de facto* refugia and ecological traps across Limpopo. I then assessed offtake at three geographical scales (i.e., districts, municipalities, and catchments) using trophy hunting permit records alone, and then in combination with problem leopard permit records, to investigate the compounding effect of additional forms of offtake and the potential for management scale mismatching. I demonstrated that high leopard offtake created fewer areas of refuge than ecological traps—resulting in vast clusters of leopard habitat under extreme hunting pressure. Furthermore, refugia were smaller in size and within close proximity of ecological traps. Given the dispersal capabilities of leopards (Fattebert *et al.* 2013; 2015), my findings raise concerns over the ability of refugia to act as potential 'safe havens'. Dispersal is a key component within source–sink dynamics (Gundersen *et al.* 2001), and often highlighted as a conservation imperative (Robinson *et al.* 2008). Yet, in the case of leopards, should connectivity between vast areas exist (investigated in Chapter 4) then the high degree of human-mediated mortality I document is likely to have significant detrimental impacts on leopard population persistence. I further demonstrated that human-mediated leopard mortality occurred mostly in prime leopard habitat. This finding has significant conservation importance, since, not only is the efficacy of potential 'safe havens' likely compromised, but any areas of high habitat suitability are likely contributing to maladaptive habitat selection in leopards (Delibes-Mateos, Ferreras & Gaona 2001; Gilroy & Sutherland 2007). To counter these issues, I concluded that management at finer-scaled units (i.e., geographical catchments) resulted in fewer ecological traps and more refugia, and should theoretically enable authorities to focus conservation attention in areas of concern. Since carnivore management is generally logistically challenging and costly (Balme, Hunter & Slotow 2009; Martin *et al.* 2012), these findings demonstrate an important management consideration; scale represents a key component of any management framework, and should be carefully considered when implementing any form of management strategy (Delsink *et al.* 2013). Moreover, regardless of the spatial distribution of hunting effort and associated deleterious effects, I further demonstrated that human-mediated leopard mortality exceeds sustainable levels determined by previous research (Caro *et al.* 2009). To improve leopard management in Limpopo, I recommended an adaptive, science-based approach to leopard management; specifically: (1) shift leopard management to a smaller scale (i.e., ecological justified geographical catchments), (2) account for problem leopard offtake, (3) undertake a local context specific modelling exercise on an annual basis to better define the level of sustainable offtake (the focus of Chapter 5), and (4) use this sustainable offtake rate to identify and reduce the number of ecological traps. These recommendations represent a 'first-step' in improved management of leopards across Limpopo; the foundations of which could easily be applied to other wide-ranging species that undergo harvest or population control.

## 6.2 MEASURING CONFLICT

Game ranching has become synonymous with private- and community-based natural resource management (Bothma, Suich & Spenceley 2009), and is largely perceived to benefit biodiversity (Lindsey, Romanach & Davies-Mostert 2009a). However, in Chapter 3, I highlighted the hidden costs of local decision-making in the absence of centralized governance and evidence-based best practice. I demonstrated that game ranching represents a highly lucrative sector within the agricultural industry, primarily due to a devolutionary shift in natural resource management over the past four decades (Parker, Thapa & Jacob 2015) and the subsequent adoption of intensive game ranching practices that facilitate high-value game breeding (Pitman *et al.* 2016). The increased investment required to breed high-value game species, together with the significant returns on investment, have resulted in increased adoption of predator-proof fencing and decreased tolerance of nuisance wildlife (Pitman *et al.* 2016). Furthermore, I demonstrated that the proportional increase in problem animal control of nuisance wildlife has far outweighed the proportional increase in game ranching trends towards more intensive practices. This likely indicates that intolerance towards nuisance wildlife is growing in momentum. My findings highlighted how large-scale changes in land-use practices—even those typically considered conservation-orientated—can have significant detrimental impacts on wildlife conservation, and further demonstrates why decisions made at the policy level should be grounded in science-based evidence. The global economic crisis of 2008—which originated in the United States of America (Allen & Giovannetti 2010)—caused significant financial impacts on South Africa's primary, secondary, and tertiary industries. Decreased tolerance among landowners towards putative problem animals has long been highlighted (Lindsey, Romanach & Davies-Mostert 2009b; Lindsey *et al.* 2013c), and is now of particular relevance given the increased economic reliance on agricultural productivity together with the increased financial risk associated with intensive high-value game breeding. Chapter 3 therefore highlighted how macro-economics can play an important role in wildlife conservation. By bestowing custodial rights of wildlife to individual property owners, legislative policies have encouraged innovation among private and communal sectors and ultimately inflicted a significant cost to wildlife conservation. In this chapter, I recommend that devolution-based natural resource management likely requires increased centralized regulation to limit, or better control, the widespread adoption of intensive game ranching practices and their negative consequences on large scale conservation objectives.

## 6.3 CONNECTING DATASETS AND SCALES

Measuring connectivity is challenging (Zeller, McGarigal & Whiteley 2012), and therefore, often poorly integrated within wildlife management. In Chapter 4, I estimated resource use and landscape connectivity across Limpopo—a key leopard stronghold—using a range of datasets to counter data deficiencies inherent in carnivore management. I adopted a range of statistical methods to overcome significant methodological limitations. Namely, I employed occupancy modelling to reduce the prevalence of false absences when modelling resource use across broad scales (Gu & Swihart 2004). I then estimated resource selection at multiple scales to overcome issues of scale dependency inherent in large mammal resource selection (Boyce 2006). Lastly, I estimated landscape-scale habitat connectivity by adopting a novel approach independent of *a priori* source and sink locations using circuit theory (Koen *et al.* 2014). Chapter 4 demonstrated that leopards exhibit markedly different scale dependent habitat relationships. This finding highlighted the importance of considering the scale at which future research is conducted (consistent with Chapter 2), and how scale relates to the specific research question being investigated. The multi-data, multi-scale approach I adopted in this chapter resulted in accurate predictions of resource use, even when integrated across multiple orders of resource selection. This approach therefore accommodates complex wildlife-habitat relationships within a single framework capable of generating accurate predictions of resource use necessary for fine- and coarse-scale management objectives. Furthermore, the scale-integrated depiction of leopard resource selection I developed in this chapter was then used to develop a landscape-scale representation of habitat connectivity (Koen *et al.* 2014). In contrast to other published connectivity analyses, my approach did not rely on prior knowledge of source or sink locations typically used to represent points of origin or destination during connectivity analyses (Zeller, McGarigal & Whiteley 2012). Instead, connectivity was measured in every possible direction. Because this approach ensures connectivity is not 'forced' from one point to another, it has the advantage of developing an unbiased landscape-scale depiction of habitat connectivity whilst avoiding tentative behavioural assumptions (Koen *et al.* 2014). As a result, I identified key linkages in need of targeted management and further relate connectivity metrics to leopard management units (LMUs) across Limpopo (a focus of Chapter 2; i.e., ecologically justified geographical catchments). This approach demonstrated how conservation authorities could easily incorporate knowledge of habitat connectivity within their current management framework. The moderate degree of connectivity detected across Limpopo suggests that although numerous ‘ecological traps’ exist (demonstrated in Chapter 2), connectivity between them remains fairly poor. Although this has negative implications for population persistence with regard to genetic exchange and species’ resilience towards disturbance, it confers some advantage insofar as leopards might remain somewhat isolated from large-scale source-sink dynamics that would be at play if high degrees of connectivity did exist. As a final assessment, I evaluated whether occupancy modelling on its own was capable of accurately informing habitat connectivity without the need for complex data analyses (e.g., resource selection functions and electrical circuit theory) and datasets that are expensive and logistically challenging to collect (e.g., GPS collar data or camera-trapping data). However, I did not find support for the use of occupancy modelling as a proxy for landscape-scale habitat connectivity. This finding has important implications for landscape-scale corridor assessments for large carnivores, and perhaps more widely (e.g., this approach has been used for jaguar *Panthera onca* corridor delineation; Zeller et al. 2012). Management authorities typically seek to conduct research in a cost effective manner, which makes occupancy modelling a favourable option (Zeller *et al.* 2011; Zeller, McGarigal & Whiteley 2012). However, I demonstrate caution against this. More research is therefore needed to evaluate the relationship between occupancy modelling and broad-scale habitat connectivity.

## 6.4 SUSTAINABLE HUNTING

Obtaining robust data to guide terrestrial hunting systems remains a major challenge for management authorities, and often results in ad hoc hunting policies and unsustainable hunting practices. In Chapter 5, I examine how leopards *Panthera pardus* respond to different levels of hunting pressure, using over forty years of demographic data, to investigate the most biologically sustainable hunting strategies. This investigation is vital, since the removal of important demographic classes can detrimentally impact population persistence, and ultimately compromise the sustainability of hunting (Milner, Nilsen & Andreassen 2007; Packer *et al.* 2009; 2011). This is particularly evident for large carnivores, such as leopards (Caro *et al.* 2009), which exhibit a polygynous mating system at risk of high levels of infanticide due to over-harvest (Balme *et al.* 2012; Balme, Hunter & Braczkowski 2012; Balme & Hunter 2013). In addition to hunting, illegal killing and state-sanctioned lethal control of putative problem animals represent additive forms of mortality, which are often ignored when devising hunting regulations. I therefore incorporated multiple forms of anthropogenic mortality to simulate realistic human-mediated pressures imposed on leopards. This analysis represents the most comprehensive attempt to model leopard demographics to date.

My results demonstrated that hunting always resulted in some degree of population decline, of which the most severe involved harvesting of female cohorts ≥7 years or male cohorts <7 years. More importantly, when accounting for minimum aging error (9%), hunting of ≥7 year hunting male leopards resulted in continued population declines. These findings highlighted important inconsistencies with previous research, which suggested that quota setting restrictions for leopards are not necessary, and that hunting practices could be solely based on unrestrictive age minimum criteria (i.e., removal of 100% of males ≥7 years old; Packer et al. 2009). Rather, I demonstrate that hunting practices—and quota-setting restrictions in particular—still need to be conservative (following the precautionary principle until more advanced modelling mehods are available). For example, when considering a reduced rate of additional mortality (1%; illegal killing or problem animal control) under a ≥7 year hunting scenario, leopard populations decline markedly even as harvest rates are reduced from 100% to 10%. Similar population trends were detected when two- or three-year recovery periods (i.e., intermittent moratoria on hunting) were implemented; in large part because the simulated leopard population was not able to sufficiently recover from high degrees of hunting. I further demonstrated that even when additive forms of mortality are held at reduced levels (i.e., illegal killing and problem animal control at 1%), population projections continue to decline even as harvest rates of males ≥7 years are reduced to 10%. Only once all forms of additive mortality are removed, together with the implementation of a 40% harvest rate with a minimum level of aging error (9%), do we identify a potentially sustainable hunting scenario. This harvest scenario would theoretically permit the removal of ~82 male leopards ≥ 7 years each year, but assumes no additional human-mediated mortality occurs (which remains an unrealistic assumption).

My findings highlighted the importance of considering multiple forms of additional mortality as well as potential inconsistencies in aging leopards to better understand the impacts of hunting on leopard populations. For leopard hunting to support or even promote population persistence, additional forms of anthropogenic mortality should be reduced (<1%). These expectations are, however, highly unlikely. Given the economic climate across leopard range (especially in Africa), it is evident that landowner tolerance of large carnivores, and particularly leopards, is decreasing as land-use practices move towards more intensive, and highly lucrative farming practices (demonstrated in Chapter 3; Pitman et al. 2016). The incorporation of aging error—a metric not used in previous leopard demographic simulations—into hunting projections further exacerbates unsustainable hunting practices, and demonstrates that even if hunters are highly proficient at aging leopards in the field, the underlying error associated with aging leopards using key phenotypic traits (Balme, Hunter & Braczkowski 2012) imposes a concerning degree of risk on leopard population persistence.

## 6.5 CHALLENGES AND FUTURE RESEARCH

In Chapter 2, I identified a large number of ecological traps across Limpopo where human-mediated mortality was high (Pitman *et al.* 2015). By definition, these ecological traps are likely attracting leopards from adjacent suboptimal habitats (Gilroy & Sutherland 2007). Although beyond the scope of my research, it would be beneficial to evaluate leopard immigration and emigration rates across Limpopo to better understand leopard population dynamics and how they are impacted by human disturbance. This could be achieved by conducting open population modelling exercises within a spatially explicit framework using capture-recapture data from camera-trapping studies (Gardner *et al.* 2010a). Furthermore, at a broader scale, dynamic occupancy modelling (using detection/non-detection data) could prove useful if capture-recapture data were not available (Kéry, Guillera-Arroita & Lahoz-Monfort 2013). These data (i.e., province-wide camera-trapping data and occupancy data) have only recently become available for Limpopo, and further afield (R T Pitman & G A Balme, *unpublished data*).

The focus of Chapter 2 was to evaluate the extent and spatial distribution of legal anthropogenic offtake of leopards in Limpopo. We limited offtake to include incidents of trophy hunting and problem animal control permits since these were the only reliable data sets available. As acknowledged in Chapter 2 (Section 6.3.1), illegal killing is likely a far greater contributing factor (St John *et al.* 2012; Swanepoel *et al.* 2014a) towards the formation of ecological traps, however, this form of mortality could not be included. Nevertheless, it is plausible to assume that illegal killing of leopards occurs in similar locations to that of problem animal control and trophy hunting (Balme *et al.* 2010; Chapron & Treves 2016; Teichman, Cristescu & Darimont 2016). In fact, problem animal control is sometimes used as a means of removing leopards in situations where no conflict exists (R T Pitman, *personal observation*). Incorporating illegal activities would greatly enhance that identification of refugia and ecological traps across Limpopo, and therefore, future studies should attempt to quantify such levels of human-mediated disturbance (St John *et al.* 2012). In addition, I adopted an approach by Stoner et al. (2013), whereby a published sustainable harvest rate is used to distinguish refugia and ecological traps. As highlighted in the discussion of Chapter 2, a more robust approach would be advisable. One such approach would be to conduct a simulation exercise (as I conducted later in Chapter 5) to evaluate potentially sustainable hunting scenarios and subsequent offtake levels (Bunnefeld *et al.* 2013; see Edwards *et al.* 2014). These results would then feed back into the formation of refugia and ecological traps, and how to better management them.

In Chapter 3, I used annual game auction records to measure the scale and profitability of game ranching practices. This approach was adopted because records of private game sales are not available, even though the latter comprise a large proportion of the game ranching industry (Taylor, Lindsey & Davies-Mostert 2016). Inclusion of these data, if they were available, would greatly increase the the analyses of Chapter 3, and the resulting inferences. Nevertheless, game auction records are likely to reflect the status of game sales more generally (Van Der Merwe & Saayman 2003; Van Der Merwe, Saayman & Krugell 2004; Taylor, Lindsey & Davies-Mostert 2016), and therefore provided a suitable proxy. In addition, I used the number of permit applications for problem animals as a proxy for landowner tolerance. Under this assumption, I expected an increase in permit applications to correlate (negatively, and linearly) with landowner tolerance of free-ranging wildlife (i.e., as tolerance decreases, permits applications increase). It could be argued, however, that an increase in permit applications could reflect an increase in compliance to regulation, perhaps caused by increased legislative control. There is no evidence to support this latter assumption, and in fact, the opposite is more likely given the resource limitations experienced across management authorities in South Africa. The fact that leopard populations in Limpopo are declining (as demonstrated in Supporting Information S3.7), suggests the former assumption (which I follow in Chapter 3) is likely to hold true.

One of the primary causes of leopard mortality in Limpopo, and southern Africa more generally (St John *et al.* 2012), relate to state-sanctioned problem leopard control and illegal killing (Pitman *et al.* 2015; 2016). I focussed on both forms of mortality in Chapter 3 and

Chapter 5. In Chapter 3 I demonstrated the extent of reported problem leopard control in Limpopo (and their increasing trend), whilst in Chapter 5 I simulated the proportional impact of problem leopard control and illegal killing (i.e., at reduced levels; 1%). Although these analyses are beneficial to leopard management and conservation, uncertainties still remain, and in both Chapters, I fail to identify the degree to which these forms of mortality actually impact leopard populations in Limpopo. This omission is largely the result of a lack of province-wide abundance data required to estimate leopard population size, as well as rates of mortality given current population trends. To counter this challenge, future research should adopt an adaptive, science-based monitoring strategy evaluation framework (MSE; as discussed in Chapter 1) (Bunnefeld, Hoshino & Milner-Gulland 2011). The 'dynamic operating model' I present in Chapter 5 provides a starting point upon which an MSE could be based. The MSE approach is based on a suite of models about the population dynamics of a species (e.g., leopard) (Bunnefeld, Redpath & Irvine 2015). For leopards, the baseline model (e.g., dynamic operating model; Chapter 5) aims to capture the key processes of leopard population dynamics given the best biological knowledge available. The next phase of an MSE is to simulate the process of monitoring leopard, which results in simulated demographic measurements (e.g., number of individuals, distribution, sex ratios). Monitoring is always imperfect since we cannot detect all individuals (MacKenzie *et al.* 2006), particularly across large spatial scales such as Limpopo. However, within an MSE, the monitoring component is represented by the 'observation model', which explicitly accounts for error and bias in detection probabilities (Edwards *et al.* 2014). The data used in the 'observation model' are then passed to the 'management model', which comprises a set of rules (known as 'harvest control rules'; HCRs) used for determining management actions (Bunnefeld & Keane 2014b). HCRs incorporate factors such as biological and socio-economic components, stakeholder requirements, spatial and temporal restrictions (e.g., hunting zones and/or moratoriums), and harvest methods (i.e., hunting techniques) (Bunnefeld & Keane 2014b). Importantly, the success of management implementation and human-decision making can be incorporated within HCRs (Milner-Gulland 2011; Bunnefeld *et al.* 2013). This is an important addition to assessing management strategies, as resource users (e.g., professional hunters or subsistence poachers) may not fully comply with regulations, or individual behavioral dynamics of resource users might affect how a species is harvested (Milner-Gulland *et al.* 2010). These various HCRs form the 'harvester operating model', which feeds back to the 'dynamic operating model' as the model updates to the next time step. By evaluating a range of HCRs against a set of operating models using multiple performance metrics, MSE enables scientists to give resource managers advice on robust management procedures as well as simulated information on the trade-offs involved with each procedure (Bunnefeld et al. 2011). In addition, an MSE can be used to evaluate which types of data, and how much of it, should be collected to improve management performance. Furthermore, stakeholders can be involved at various points in the process of developing and evaluating different HCRs and assessment approaches (as is routinely done in fisheries research) (Fulton *et al.* 2014). Thereby trust increases among stakeholders that use a resource and the authority that governs that resource. Such an approach is likely to address many of the challenges facing large carnivore management and conservation.

In both Chapter 3 (e.g., to identify game ranching practices) and Chapter 4 (e.g., to assess leopard space use through broad-scale occupancy modelling) I used questionnaire surveys to collect requisite data. Although logistically efficient and cost effective, questionnaire surveys are prone to survey and response bias (Holbrook, Green & Krosnick 2003). For example, survey respondents may forget or misdate certain events relevant to the survey in question (Belli, Traugott & Young 1999), differences in conversation conventions and norms may lead respondents to misinterpret questions (Holbrook, Green & Krosnick 2003), or phenomenon such as social desirability bias may undermine face-to-face versus telephonic interviews (Belli, Traugott & Young 1999; Holbrook, Green & Krosnick 2003) (e.g., face-to-face interviews might generate more false positives as respondents are keen to engage in conversation about interesting topics, whereas telephonic interviews might be more realistic or perhaps generate more false negative responses). In Chapter 3, I used an online survey distributed to game ranchers across Limpopo. To reduce survey and response bias, the survey was kept very short and comprised very simple, easily understandable questions. The online survey was also translated into the two most common languages among the game ranching community. The process was completely anonymous. In Chapter 4, I used a mixture of face-to-face questionnaires surveys. To reduce survey and response bias, I ensured that the questionnaire was very short and conducted by a survey coordinator that could speak the respondents preferred language. The questionnaire comprised an additional vetting process (as discussed in section 4.3.2) to exclude respondents that were not capable to identifying leopards in the field. Respondents were only contacted by telephone if they wished to participate in the survey in the following year, and could opt out of this voluntary process at any time. All data collected by these two questionnaires were spatially and temporally independent; for example, the questionnaire survey used in Chapter 3 was distributed to game ranchers occupying discrete properties across Limpopo (i.e., respondents were not able to conduct the survey more than once), whilst in Chapter 4, the survey followed a pre-defined sampling grid.  Social desirability bias might have played of role in the occupancy questionnaire survey (Chapter 4), since two modes were used to collect data. However, the respondents that were contacted via telephone were also initially contacted through face-to-face interactions, which likely reduces to potential for social desirability bias (Holbrook, Green & Krosnick 2003).

## 6.7 CONCLUSION

My primary objective of this thesis was to significantly increase our knowledge of leopards across a vast and biodiverse region of southern Africa, and to develop practical and scientifically justified methods to facilitate accurate and efficient management of the species. Although the challenges are great, and complexities vast, my scientific contributions with this thesis provide valuable insights and solutions into the fundamental components that underpin the management and conservation of the world’s most wide-ranging and persecuted felid (Hunter, Henschel & Ray 2013). Some of the major threats to leopard populations in Africa—trophy hunting, illegal killing, and state-sanctioned population control—are exemplified in Limpopo Province, South Africa; one of the poorest provinces in southern Africa (Statistics SA). Limpopo Province contains extensive leopard habitat, with widespread leopard populations (Swanepoel *et al.* 2013), and awards the largest number of trophy hunting permits across South Africa (Daly *et al.* 2005). In addition, destruction permits for leopards are also the highest in Limpopo when compared to all other South African provinces, whilst the illegal killing of leopards in Limpopo eclipses legal offtake (St John *et al.* 2012).

To counter these challenges, I developed novel solutions to meet the conservation requirements of the species, but which fell within the logistical and managerial constraints of a conservation authority operating limited budgets and a lack of capacity. I first assessed the relationship between human-mediated leopard mortality and habitat quality, and then investigated the compounding effect of multiple forms of offtake to develop an adaptive, science-based approach to leopard management that (1) spreads hunting effort more evenly, (2) shifts management to a smaller, more controllable scale, and (3) accounts for additional forms of mortality when devising hunting quotas (see Chapter 2). I then set out to investigate what the primary driver of lethal control (i.e., a significant form of additive mortality) of leopards was across Limpopo. I demonstrated that game ranching—although commonly perceived to benefit wildlife conservation—had undergone a marked shift in production towards intensive practices, leading to a significant decrease in tolerance of free-ranging wildlife, resulting in their increasing legal destruction (see Chapter 3). Given the increasing rates of leopard mortality, I then evaluated the degree of habitat connectivity across the region using a range of datasets and novel methods to counter data deficiencies and methodological limitations inherent in carnivore management and monitoring. The multi-data, multi-scale approach I present accurately predicted resource use across multiple scales of leopard habitat and empirically demonstrates how management authorities can more suitably utilise fragmentary datasets for large carnivore management. I further identified key regions across Limpopo that exhibit markedly low permeability, and determine that leopard management units across Limpopo are largely below-optimal when compared to prime leopard habitat, which warrants further conservation attention and management intervention (see Chapter 4). Lastly, I evaluated how leopards respond to different levels of hunting pressure to investigate which hunting strategies are the most biologically sustainable, whilst considering multiple forms of anthropogenic mortality (i.e., mortality drivers previously identified in Chapter 2 and Chapter 3). My findings have significant implications for leopard management insofar as isolated hunting strategies are not enough to mitigate leopard population declines. Instead, if hunting of leopards is to carry the banner of sustainable conservation practice, an integrated and adaptive approach is required, where additional forms of mortality are reduced, age-minimum male-only restrictions are implemented, with precautionary quotas, and the potential implementation of recover periods (see Chapter 5). I conclude that the findings in this thesis provide valuable information and novel guidance that could benefit the management and conservation of leopards across the region, and further afield.

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